

**DEVELOPMENT AND APPLICATION OF A
MULTISTATE MODEL TO THE
NORTHERN SUBPOPULATION OF
LOGGERHEAD SEA TURTLES (*Caretta caretta*)**

by:

Melissa E. Hedges

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Approved by:

James M. Berkson, Chair

Marcella J. Kelly, Committee Member

Nancy B. Thompson, Committee Member

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(ABSTRACT)

Loggerhead sea turtles (*Caretta caretta*) are listed as threatened under the Endangered Species Act and are protected both on nesting beaches and in United States waters. Loggerhead sea turtles are long-lived species and are most easily studied on the beaches during the nesting season. Bald Head Island, North Carolina has one of the highest density nesting beaches of loggerhead sea turtles in the turtle's northern range on the East Coast of the United States. Key life history parameters were estimated and applied to a population model using 16 years of data from a mark-recapture study on the loggerhead sea turtle nesting population on Bald Head Island, North Carolina.

The beach survey conducted on the island only allowed for the capture of adult female sea turtles during the breeding state even though females may spend multiple years in the unobservable non-breeding state. The majority of females captured over the last 16 years have never been recaptured at the original capture site. These transients in the data coupled with unobservable states violate the assumption of equal catchability in the available single state mark-recapture models. Therefore, a multistate mark-recapture model originally developed for leatherback sea turtles was applied to the Bald Head Island loggerhead population. Multistate modeling provides a new technique to estimate sea turtle demographic parameters in which all model assumptions can be met. The

multistate model outputs female survival rates, capture probability, and transition probabilities between breeding and non-breeding states. A correction factor for trap-dependence and transients was included given that both factors tested significant in the global model goodness-of-fit tests.

The estimates of annual adult survival rate and breeding transitions were then used to project population size for the northern subpopulation. For the first time, estimation error around estimates of benthic juvenile and adult survival rates was included in a loggerhead sea turtle model. I explored the effects of estimation error, three levels of clutch frequency, and larger TED openings on population growth rate and on the probability of reaching a nesting recovery threshold. The nesting recovery threshold was based upon recovery criteria from the Federal Recovery Plan and set as the probability of reaching 12,800 nests/season in the states of North Carolina, South Carolina, and Georgia within a 50 year time period. The results of this study provide important information to guide future management and research.

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CHAPTER 1 – LITERATURE REVIEW OF LOGGERHEAD SEA TURTLES

Introduction

The loggerhead sea turtle, *Caretta caretta* (Linnaeus 1758), was listed as a threatened species under the Endangered Species Act in 1978. Historically, the species had commercial value to fisherman, as it was valued for its oil and meat. In the United States sea turtles comprised one of the first commercial fisheries in the late 1800s and loggerheads were harvested from northwestern Atlantic coastal waters (Witzell 1994). However, a decline in the catch-per-unit-effort of sea turtles raised concern about the possibility of extinction, leading to federal protection. To aid in the recovery, in depth research on loggerhead sea turtle biology and ecology intensified after the species' federal listing.

Recent research has led to advances in the understanding of basic life history characteristics and vital rate estimates, and has more clearly defined the known threats to the loggerhead sea turtle. An accumulation of this information has led to the ability to create demographic population models for the loggerhead sea turtle population. Demographic models allow researchers to make predictions for populations and also to determine the impact different threats can have on the population as a whole and on individual life stages. Sea turtles are both long-lived and have a late age of sexual maturity. These life history traits make it essential to have a long time series of data, in order to create a robust population model. Tagging studies of nesting females are also extremely important to better understand the nesting behavior of loggerhead sea turtles. The data that is already available for my study meet both of those criteria.

Natural History

The loggerhead sea turtle is one of 6 extant species in the family Cheloniidae and diverged from the ridley and hawksbill sea turtles approximately 10 million years ago (Bowen 2003). Loggerheads nesting in the North Atlantic are genetically distinct from loggerheads nesting in other ocean basins, specifically the Indian and Pacific Oceans (Bowen 2003). Loggerheads nest on every continent except Antarctica and are highly migratory, resulting in an extended range thousands of miles from the nesting beaches. The loggerhead's nesting distribution is one of the most temperate when compared to other sea turtle species (Bowen 2003). Other sea turtle species more commonly inhabit and nest in areas around the tropics (Bowen 2003). The U.S. nesting aggregation of loggerheads as a whole is the second largest in the world, the largest being located on the islands of Masirah and Kuria Muria in Oman (Ehrhart 1989).

As loggerheads diverged into a distinct species, their body mass increased and they developed an oversized skull specialized for the consumption of hard-shelled benthic prey (Kamezaki 2003). The loggerhead is characterized by a reddish-brown carapace, upper shell, and can reach a weight of up to 400 pounds (Kamezaki 2003). The standardized measurement to gauge sea turtle size is a measure of the straight carapace length (SCL) measured from notch to tip. The range for adult nesting female loggerheads is between 70 and 109 cm (Dodd 1988). Males are typically larger by mass, have a longer carapace, a longer tail, and a larger curved claw on each forelimb, used during mating (Kamezaki 2003). However, this sexual dimorphism is not evident until loggerheads reach sexual maturity. The males also do not return to the beach after their initial hatching period and as a result, little is known about any sex-specific behavior.

Loggerheads also do not utilize the large maxillae until adulthood, at which point dominant prey species shift from coelenterates and salps to benthic species (Bjorndal 1997, Kamezaki 2003). The most common prey species include horseshoe crabs (*Limulus polyphemus*), whelks (family Buccinidae), conchs (family Strombidae), spider crabs (*Libinia dubia*), lady crabs (*Ovalipes ocellatus*), hermit crabs (family Diogenidae), and other slow-moving invertebrates (Hopkins-Murphy et al. 2003). The dominant prey species for loggerheads is correlated to the location of its feeding grounds because inshore habitat characteristics vary drastically along the East coast. The Chesapeake Bay provides an abundance of horseshoe crabs and blue crabs as a food source whereas the sounds of North Carolina are inundated by freshwater and provide prey species such as whelks and other crab species (Hopkins-Murphy et al. 2003).

Life History

Breeding

The geographic range for loggerheads within a single population varies spatially and temporally by age class, sex, and the origin of hatching. Nesting beaches in the U.S. range from southern Virginia, around the Gulf coast to the beaches of Texas. While Florida receives the highest density of nesting females, other key areas are the barrier islands of North Carolina, South Carolina, and Georgia (Hopkins and Richardson 1984). A suitable nesting beach is usually characterized by a wide, sandy, open beach leading to low dunes and a flat approach to the ocean (Miller et al. 2003). Nests must be laid above the high tide line to avoid tidal inundation and drowning of the eggs. Well-ventilated

substrate, low salinity, and high humidity are all necessary for successful development of the embryos (Miller et al. 2003).

Beginning in April, both male and female loggerheads migrate to the vicinity of breeding grounds. Males make this migration on a yearly basis (Miller 1997), whereas the observed nesting remigration interval for females averages every two to three years (Schroeder et al. 2003). Mating occurs in the vicinity of the nesting beach and may last up to six weeks, after which males return to the foraging grounds and females continue on to the nesting grounds (Miller et al. 2003).

Loggerheads navigate to the breeding grounds using an internal magnetic compass, specifically finding locations through changes in magnetic inclinations (Limpus et al. 1992, Schroeder et al. 2003). As a result, females are philopatric, returning to the general geographic area of their natal beach to nest (Carr 1975), and also exhibit nest site fidelity, nesting within the same geographic area each breeding season (Schroeder et al. 2003). Nest site choice is believed to be nonrandom, although no study has shown a pattern for a female's choice of nest site. On average the observed distance between nest sites within one nesting season for an individual female is 5km or less, but ranges from 0 to 95 km in the U.S. (Miller et al. 2003). Because of the loggerhead's large body mass, nests are only laid at night to prevent dehydration and overheating during the summer months (Spotila and Standora 1985).

Females store enough sperm in their oviducts for the entire nesting season, during which time they lay between one and seven clutches, with a period of 12-16 days between each nesting event (Caldwell 1962, Dodd 1988). The average clutch size is 112.4 eggs, but ranges from 23-198 eggs (Van Buskirk and Crowder 1994). Egg fertility

for loggerheads is usually greater than 80%, but position of the nest on the beach affects hatchling sex ratio, fitness of hatchlings, and emergence success (Miller et al. 2003). Observational studies indicate that there is a decrease in an individual's reproductive output as a nesting season progresses, with the fifth clutch of the season being on average 38% smaller than the first four clutches (Broderick et al. 2003). Neophyte turtles have been found to lay smaller clutches than remigrants (Hawkes et al. 2005). Incubation lasts on average from 40-70 days along the northwestern Atlantic coast, increasing as latitude increases (National Research Council 1990). The average loggerhead nest has a hatching success rate of greater than 80% (National Research Council 1990). However, the percent of loggerhead hatchlings that survive from hatching to emergence from the nest is typically lower than the actual hatching rate because of the challenge of climbing to the beach surface (Miller et al. 2003).

For loggerheads, as with many other reptiles, sex is determined by temperature (Yntema and Mrosovsky 1980). A warmer climate, or warmer location within the nest, produces more females, where colder temperatures produce a higher proportion of males per clutch. Estimates of sex ratios for each nesting subpopulation have been obtained through juvenile sexing. The most recently published paper estimates that the mean annual sex ratio is 58% female for nests laid on Bald Head Island, North Carolina (Hawkes et al. 2007). The study used temperature loggers to record sand temperatures during the length of the nesting season and modeled the sex ratio using the known pivotal temperatures for sex determination in loggerhead sea turtles. This study produced the first estimates of sex ratios from nests on Bald Head Island, North Carolina. One other recent study estimated sex ratios by rearing hatchlings in the lab until laparoscopies could be

performed to determine the sex and found similar results to those in Hawkes et al. (2007) (Jeanette Wyneken, pers. comm..)

Samples of hatchlings were taken from nests laid in 2002 and 2003 to estimate sex ratios in both the northern and southern subpopulations (Wyneken et al. 2003). In 2002, an overall t-test of all sample sites within the northern and southern subpopulations showed no significant difference in sex ratios. When the t-tests were broken into three sampling periods (early season, mid season, and late season) significant differences appeared for the first two periods. The northern subpopulation produced significantly more females in the early and mid seasons, and the southern subpopulation produced significantly more females in the late season. In 2003, however, the t-test between northern and southern populations showed that significantly fewer females were produced by the northern subpopulation. The only significant periodic trend in these data is from the mid season, showing significantly fewer females produced from the northern subpopulation. These findings suggest that loggerhead sex may not be as easily determined as previous literature suggests. Data from 2002 indicate that the northern subpopulation can contribute up to 100% females per nest (Jeanette Wyneken pers. comm.). The results of the above study must be interpreted with caution because of low sample sizes in both the number of clutches sampled and the number of years sampled. However, both the estimates from Wyneken et al. (2003) and Hawkes et al. (2007) differ from past literature which suggested the northern subpopulation may produce up to 65% males annually (NMFS-SEFSC 2001). The new estimates of sex ratios can greatly impact population models if subpopulations are parameterized with a sex ratio skewed in the wrong direction

Juvenile Development and Migrations

Immediately after emerging from the nest, hatchlings enter a twenty-four hour “swimming frenzy” to reach the North Atlantic Gyre, the clockwise flowing current in the northern Atlantic Ocean (Lohmann and Lohmann 2003) (Figure 1.1). The hatchlings from U.S. beaches make an initial migration to the eastern Atlantic within the floating *Sargassum* seaweed community. The discovery of this migration to the Azores and Madeira, a period in loggerhead sea turtle development formerly known as the “lost years,” was recently discovered through a tagging project initiated by the Archie Carr Center for Sea Turtle Research at the University of Florida (Bjorndal et al. 1994). Juvenile oceanic loggerheads initially tagged in the Azores were recaptured off the coast of the eastern U.S., indicating that loggerheads hatching on U.S. beaches do in fact make a trans-Atlantic migration. However, the evolutionary function for this migration is still unknown.

Juvenile loggerheads follow the North Atlantic Gyre back to the western Atlantic after spending 6.5 – 11 (average 8.2) years in the Azores and enter the neritic zones along the U.S. East coast (Bjorndal et al. 2000b). The neritic zone extends to waters of up to 200m depth, usually correlated with the continental shelf, and is referred to as the turtles’ “foraging grounds.”

The geographic range of foraging grounds extends beyond the nesting area from the Long Island Sound to the Gulf of Mexico (Butler et al. 1987). Loggerheads migrate from their foraging grounds to warmer waters annually based on thermoregulatory needs (Hopkins-Murphy et al. 2003). In the fall loggerheads migrate both south and offshore, shifting the entire distribution of loggerheads south for the winter months. Loggerheads

migrate back to northern foraging grounds in the spring, but must also migrate from foraging to nesting grounds during the later spring months. While the breeding grounds for loggerheads are distinct, turtles from different nesting subpopulations intermix on the foraging grounds (Schroeder et al. 2003).

Subpopulations in the southeastern United States

Through mtDNA analysis, Bowen et al. (1993), concluded that there are at least two genetically distinct subpopulations of loggerheads nesting in the eastern United States. Mitochondrial DNA is only maternally inherited and does not account for the fact that gene flow may be male-mediated (Bowen et al. 2003). However, based on the mtDNA work from Bowen (1993, 1995), the U.S. NMFS's Turtle Expert Working Group (TEWG 1998) classifies the North Atlantic nesting aggregation into five nesting subpopulations (Figure 1.2). The nesting subpopulations are used as management or recovery units within the loggerhead sea turtle recovery plan. The boundaries for the subpopulations are, (1) northern nesting subpopulation (Hatteras, North Carolina to Cape Canaveral, Florida; (2) South Florida nesting subpopulation (Cape Canaveral to Naples, Florida); (3) Florida Panhandle nesting subpopulation (Eglin Air Force Base to Panama City, Florida); (4) Dry Tortugas nesting subpopulation; and (5) Yucatan peninsula nesting subpopulation (eastern Yucatan, Mexico) (TEWG 1998, 2000).

One genetic study however, showed no difference in mitochondrial DNA sequences between nesting aggregations unless they were separated by 100km of beach with no nesting areas in between (Francisco-Pearce 2001). This may be explained by one theory that suggests nesting habitats are dynamic on an evolutionary time scale, shifting

as the climate, sea level, and geography of nesting beaches change (Bowen 2003). The possibility exists that the northern subpopulation was only recently colonized and not enough time has passed for mtDNA sequences to diverge at a detectable level.

Analysis of biparentally inherited nuclear DNA from multiple nesting beaches on the East of the US revealed very low population structure (Bowen et al. 2005). After Bonferroni correction for multiple tests, all but one pairwise comparison of microsatellite loci between the eight US nesting locations were nonsignificant. The comparison between northwest Florida and Georgia nesting aggregations remained significant after applying the Bonferroni correction. If viewed independently, these results from mtDNA and nDNA analyses reveal very different levels of population structure for loggerhead sea turtles in the northwestern Atlantic. While study of haplotypes and microsatellites expose the complexity of the loggerhead's genetic population dynamics, they are only one line of evidence necessary to understand the full spectrum of the complex population. An understanding of subpopulation mixing as well as the extent of male mediated gene flow are still needed.

Population Estimations

To better understand female loggerhead site fidelity and the number of females nesting at specific locations, nest counts are needed as is the identification of individual females. The Index Nesting Beach Survey (INBS) program provides data on number of nests laid per year from 1989-2006. The number of nests is recorded by individual states and the results are broken into nest counts by subpopulation. The northern nesting subpopulation produces 4,370 to 7,887 nests annually, representing about 1,524 nesting

females per year if females each lay an average of 4.1 nests/season (TEWG 2000). The TEWG report describes the number of nests for the northern subpopulation as stable or declining; yet, the data indicate no statistically significant decline in the number of nests. The South Florida subpopulation annual nest counts range from 48,531 to 83,442, representing 32,000 to 56,000 nesting females annually from 1989 to 1998. However, data from 2001 to 2001 indicate a 22.3% decline in nests from 1989 to 2005. From 2001 to 2005 only an average of 14,423 loggerhead nests were laid on Florida Beaches (Florida Fish and Wildlife Research Institute 2006). The Florida Panhandle subpopulation's nests range from 113 to 1285 per year. The Dry Tortugas subpopulation produces 184 to 270 nests annually. Little nesting data exists for the Yucatan subpopulation, but there were 1,052 nests recorded in 1998. The time series of data for the Dry Tortugas and the Yucatan subpopulation are too short to detect nesting trends.

For most of these nesting beaches, only morning nest counts are conducted. Because of individual variability among female loggerheads, the morning nest counts alone do not provide the necessary information needed to determine the number of females nesting on a particular beach or the number of years between active breeding seasons (Schroeder et al. 2003). A census of nesting females with identification of each female is necessary to detect trends in the number of nesting females, recruitment of females into the population, and fecundity per individual female. However, studies such as these require a long time series. Loggerheads are long-lived iteroparous species and do not sexually mature until they reach a specific size, estimated at 87cm SCL (straight carapace length) or approximately 35 years of age (Snover 2002). Because of the late age at sexual maturity a long time series is required to follow an entire cohort through time to

sexual maturity. Consequently, current data sets spanning 25 years may not be long enough to detect trends in population size due to the time required to follow a cohort through time. It has been suggested that no fewer than 30 to 50 data points be collected to sufficiently analyze and statistically detect changes in a time series analysis (Yaffe and McGee 2000).

Population Status and Management

The loggerhead sea turtle is listed as threatened/endangered at three different political levels. The Red List published by The World Conservation Union (IUCN) lists all populations of the species *Caretta caretta* as endangered over its entire international range (MTSG 1996). The IUCN listing does not have any bearing on the actual management of the species or recovery plans. The Convention for International Trade of Endangered Species (CITES) protects against the international trade of sea turtles, or any part thereof, and currently has 167 member nations (CITES 2005). CITES is the most well recognized international treaty for sea turtle protection and participation to CITES is voluntary (Tiwari 2002). However, in some developing nations, as well as the Cayman Islands, the trade of sea turtles occurs within a country's political boundaries, in which case the treaty is not violated. There are numerous other international treaties and conventions for the conservation of sea turtles such as the Convention on the Conservation of Migratory Species of Wild Animals (CMS) and the Inter-American Convention for the Protection of Sea Turtles (IAC) (Tiwari 2002). These international efforts are critical to the protection of sea turtles, especially during their geographically expansive migrations.

Listing of sea turtles in the U.S. occurs at both the state and federal levels. All coastal states in which loggerheads inhabit state waters/beaches list the loggerhead as a threatened species and may have stricter laws for the species' protection than those set forth by the federal government. In the U.S., the Endangered Species Act of 1973 (ESA) supersedes all state or local laws. The loggerhead sea turtle was first listed as threatened under the ESA in June of 1978 when scientists noticed reduced nesting of females on coastal beaches (FWS 1978, 43 FR 38200). The listing category of "threatened" implies that the species has the potential to reach endangered status in the near future. The ESA protects loggerhead sea turtles in United States waters, while nesting on United States beaches, and also prevents importation of the sea turtles or parts thereof from foreign countries. After the inception of the ESA, the legal trade of sea turtles within the United States halted, and poaching of sea turtles in the United States exists at a minimal level. However, turtles with nesting sites within the United States may be poached in international waters during seasonal migrations.

Loggerhead sea turtles' unique life history characteristics require both the National Marine Fisheries Service (NMFS) and the United States Fish and Wildlife Service (USFWS) to share responsibility for the management of sea turtles in the United States and its waters. The USFWS and state wildlife agencies take responsibility for enforcing protection of turtle nesting beaches and the NMFS takes primary responsibility for protection of the species in the water.

While the protection of sea turtles rests with the ESA, there is a fine line between the direct and indirect impacts on the species. Section 9 of the ESA prohibits any person to "harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect, or attempt to

engage in any such conduct” any sea turtle species both on land and in the U.S. waters (Public Law 93-205). Currently under debate is whether beachfront lighting and vehicular driving on beaches have a direct negative impact on loggerhead sea turtle populations. As a result, the extent of sea turtle conservation measures can rest heavily with local governments as well as private landowners.

In 2002, NMFS received a petition from environmental groups to reclassify the northern subpopulation and Florida Panhandle subpopulation of loggerheads from “threatened” to “endangered” under the ESA, granted that there are distinct population segments in the western Atlantic nesting aggregation. The National Marine Fisheries Service denied the petition for re-listing based on the fact that there is no robust data to declare the northern and Florida Panhandle subpopulations as distinct population segments (FWS and NOAA 2003).

Threats

Additive causes of mortality raise concern for species listed under the ESA and may increase the rate of decline of the population. Anthropogenic threats to loggerhead sea turtles affect mortality rates of every life stage. The life stages of eggs, hatchlings, and adult females are impacted by threats in both the terrestrial and aquatic habitats and all other life stages are affected by threats in aquatic habitats. The most common terrestrial threat to sea turtles is habitat degradation of the nesting beach. Sources of habitat degradation include light pollution, dredging and beach nourishment (introduction of new sand to create larger beaches), and construction of sea walls or other permanent objects on the beach. In the water, loggerhead sea turtles are a large component of the

bycatch associated with fisheries that trawl or use longline gear. Bycatch is all the species captured by fishing gear that are not the target species for the fishery. For example, the longline fishery typically targets tuna or swordfish in the western Atlantic. The bycatch species for this fishery are all species that are neither tuna nor swordfish. These sources of mortality may pose threats to loggerhead sea turtle population.

Beach Habitat Degradation

While loggerheads do not spend a large portion of their life on the beach, suitable nesting habitat is essential. Alterations to the beach are both natural and human induced and may block the path of a female, making it difficult to find a suitable nest site. Natural alterations include beach erosion and accretion caused by the natural movement of barrier islands and hurricanes (National Research Council 1990). However, these processes can be accelerated by altering natural processes of tides and wave action with jetties, permanent sandbags, and a variety of other manmade structures.

Human induced habitat degradation on the beach includes channel dredging, beach nourishment, vehicular use on beach, sea walls, and light pollution related to beachfront property development. Beach nourishment is an increasing trend, especially on barrier islands where the beach has high intrinsic value and economic value to homeowners and businesses (Trembanis et al. 1999). Beach nourishment is a two stage process involving dredging sediment from a channel bottom and placing that sediment on an existing beach. Channels are often dredged for nautical traffic such as in the Intercoastal Waterway and major shipping channels. Channel dredging requires pumping bottom sand, often from estuaries, and depositing the sand in other locations, often on

beaches where sand is needed to counter erosion (Greene 2002). Dredging requires weeks or months to complete, with work commonly occurring 24 hours a day. Permits for this work not only consider sea turtle presence, but also a number of anadromous fish that enter estuaries to spawn. Dredging activities can result in a loss of foraging habitat for both sexes of sea turtles prior to mating when they are often found in estuaries (National Research Council 1990). The lights, pipes, heavy machinery, and extra human presence on the beach have the most potential to disrupt or harm nesting females during the summer months.

While beach nourishment has the potential to increase the area of nesting habitat by lengthening and widening the beach, the quality of substrate used for nourishment can present problems (Crain et al. 1995). Physical properties of the substrate that are important both to nesting females in site selection and the development of embryos include sand-grain size, grain shape, silt-clay content, sand color, beach compaction, moisture content, mineral content, substrate water potential, and porosity/gas diffusion (Nelson 1992). Areas dredged are usually estuaries, harbors, and channels, all of which act as environmental “sinks” for toxins, runoff, and other contaminants (Crain et al. 1995). The effects of these toxins on embryo development are unknown, but may slow or terminate development. Nourished beaches have also been shown to retain more water, which can result in the drowning of embryos if the nest is inundated with water (Parkinson et al. 1994). Another example of a change in the nest environment is the color of the substrate used for nourishment. An alteration in the color changes the heat absorption properties of the substrate and can significantly alter the temperature within the nest chamber (Crain et al. 1995). Sea turtle embryos must develop within a particular

range of temperatures. This range also determines the sex ratio within a nest, which may be critical to maintaining the current population structure (Miller et al. 2003). The properties of the nourished substrate not only affect embryo development, but also the capability of a female to find suitable nesting habitat.

Degraded nesting habitat for females includes the deposition of hard substrate onto the beaches, changes in substrate composition, temperature and humidity, and the overall slope of the beach (Crain et al. 1995). It is thought that the females rely on visual cues to locate a nest site, and may never leave the surf if a beach is rejected as a nesting site (Rumbold et al. 2001). One study of Japanese nesting sites found, through a forward variable selection process, that sand softness, distance from nearest human community, presence of lagoons, and beach height have positive effects on nest site selection (Kikukawa et al. 1999). For example, if the substrate on the beach is compacted, the female will have a harder time digging a nest and may abandon any nesting attempt. It remains difficult to quantify the effect of nourishment on turtle nests because sea turtles often inspect the beach before emerging from the ocean; therefore, the number of false crawls may be a misleading variable in site selection studies (Rumbold et al. 2001). A comparison of the number of nests per beach of nourished and non-nourished beaches also presents experimental design difficulties (Rumbold et al. 2001). When females do not nest on the nourished beach, they may turn to surrounding or suboptimal beaches to lay nests.

Three other anthropogenic effects that reduce female nesting are sea walls, recreational driving on the beach, and beachfront lighting. The creation of sea walls eliminates any former nesting ground available to sea turtles by removing the dune line

and decreasing beach length. This forces females to deposit nests below the high tide line and this usually results in 100% mortality due to flooding of the nest (National Research Council 1990).

The use of vehicles on nesting beaches presents multiple problems, including running over both females and hatchlings (Hosier 1981). Deep tire tracks may trap hatchlings or disorient them away from the ocean by obstructing their view to the ocean (Hosier 1981). Headlights at night will also disorient hatchlings and discourage females to come ashore to nest (National Research Council 1990). When research vehicles are used during sea turtle nesting season, such as on Bald Head Island, North Carolina, the headlights are modified to a wavelength less visible to loggerhead sea turtles.

Vehicles are not the only source of artificial lighting; light associated with beachfront buildings affect the navigation of both hatchlings and nesting females. Female turtles in Florida reduce nesting attempts on beaches when light is visible from the ocean (Witherington and Martin 1996). Turtles are then forced to nest outside their preferred habitat, often on less suitable beaches. If a female turtle does not find suitable nesting habitat after several attempts, she will discharge the eggs in the ocean (National Research Council 1990). Sea-finding ability after nesting is also compromised by artificial lighting, resulting in disorientation (Witherington and Martin 1996). Evidence supports the theory that hatchlings rely on visual cues to reach the ocean from the nest site, orienting to the brightest light source. Disorientation due to artificial lighting increases the time spent on the beach, depletes critical energy stores, and increases the probability of mortality from predation, dehydration, and starvation (Witherington 1999).

Unfortunately, light pollution is a problem that has to be resolved at the local government level. Some municipalities have issued lighting ordinances requiring “turtle safe lighting” during nesting and hatching season on beachfront property. An alternative to no outside lighting are sodium ion or mercury lights which have reduced visibility to sea turtles. Out of all sea turtle species, only loggerheads are xanthophobic (Godfrey pers. comm.). Therefore, if loggerheads are the only species of concern yellow lighting is an additional alternative to white lights. However, most communities rely on voluntary recommendations that beach front lights be turned out and curtains in hotel rooms closed during nesting season. Less visible and harder to manage are the anthropogenic effects that occur past the tide line and in the open ocean.

Fisheries

Trawl Fishery

Threats in the aquatic habitat stem from a variety of sources, but direct and indirect interactions with fisheries are now the central focus in loggerhead sea turtle management. Sea turtles have the potential to interact with multiple fisheries, but longline and trawl operations pose the greatest threats (National Research Council 1990).

Trawling in the western Atlantic off the coast of the U.S. is most often used in the flounder and shrimp fisheries. Shrimp are fished from Cape Hatteras, North Carolina south to the Mexican border, which overlaps with loggerhead nesting distribution (National Research Council 1990). The shrimp fishery is most active during the summer months, a time when higher concentrations of sea turtles inhabit areas close to the shore,

overlapping spatial distribution with commercial shrimp species (National Research Council 1990).

The National Research Council (1990) estimated mortality from shrimp trawls at between 5,000-50,000 loggerheads in United States waters per year. Of 78 published papers discussing sea turtle population declines, 83% point to the shrimp fishery as a major source of loggerhead mortality.

To reduce capture rates from trawls, NMFS developed the turtle excluder device (TED). The TED provides an escape hatch for sea turtles at the cod end of the net while allowing targeted species to move through the trawl. The use of TEDs began as a voluntary gear change, but did not prove successful. Few states did however, require the TEDs within state waters before there was enough support to pass federal legislation. The federal government required the seasonal use of TEDs in 1989 and year round use in 1994 for the shrimp industry and full time use for winter trawl of the summer flounder fishery in 1992 (Crowder et al. 1994). Epperly and Teas (2002) found that the escape opening measurements set forth in the 1994 TED requirements (Federal Register 1993) were not large enough for larger juveniles and some adult to escape. An analysis of stranding data after the implementation of TEDs revealed that stranded loggerheads were larger than dimensions required for the escape opening. As of April 15, 2003, NMFS required the use of TEDs with larger opening to decrease the capture rate of larger loggerhead and green turtles as well as leatherbacks in the shrimp trawl fishery (NOAA 2003).

Information regarding the success of TEDs relies primarily on stranding data, which in itself has a large associated error, including vast changes in observer effort over

the years. Strandings only account for turtles that died near inshore waters and then washed ashore or were observed floating on the water. An analysis of stranding data from 1980-1997 concluded a significant reduction in loggerhead sea turtle strandings by 40% in South Carolina and 58% in Georgia after the implementation of TEDs (Royle and Crowder 1998). A “TED effect” analysis performed on stranding numbers from Georgia indicated a 37% decrease in strandings during periods of TED usage, in proportion to shrimp landings (Crowder et al. 1994). This decrease in the number of strandings was estimated by comparing the number of stranding between 1990-1992, when TEDs were required seasonally, to the number of strandings in years before the use of TEDs. While TEDs provide a significant decrease in turtle strandings as indicated by time series analyses, the total number of strandings for loggerheads on the east coast of the United States has increased since 1993 (NMFS-SEFSC 2001). The causes for this increase in total strandings have not yet been determined. One possible hypothesis is the increased interaction and mortalities associated with other fisheries, such as the longline fishery.

Longline Fishery

The number of interactions in the longline fishery with loggerhead sea turtles ranges from 293-2439 individuals per year, with 50% of all interactions categorized as fatal (NMFS-SEFSC 2001). The fishing gear used in the longline fishery does not allow for immediate release, and turtle may be hooked on a line for hours, until the fishermen retrieve their set hooks. During this time a sea turtle may become stressed or entangled in the fishing line. While mortality may not occur while a turtle is hooked, metabolic

acidosis and lethal levels of anaerobic glycolysis may cause mortality after the loggerhead's release (NMFS-SEFSC 2001).

In 1996 Congress reauthorized the Magnuson-Stevens Fisheries Conservation and Management Act (FCMA) (Public Law 94-265) to include the Sustainable Fisheries Act (SFA) (Public Law 104-297) which requires minimization of bycatch in the U.S.'s managed fisheries. The SFA mandated the eight regional fisheries management councils as responsible for producing new Fisheries Management Plans (FMP) and required them to include measures to assess levels of bycatch, reduce bycatch, and reduce mortality of bycatch species when bycatch cannot be eliminated. Sea turtles have benefited through the FCMA because the negative interaction of the species with commercial/recreational fisheries must now be addressed.

In 2000, NMFS reinitiated consultation under Section 7 of the ESA to evaluate the issue of sea turtles as bycatch in the longline fishery. Bycatch is considered "take" if the species is listed, which is prohibited in Section 7 of the ESA. The resulting Biological Opinion for the Highly Migratory Species Management Plan identified longliners as cause for the species' potential extinction (NMFS 2001). In order to decrease the number of interactions between the loggerhead sea turtle and longline fisheries NMFS closed the Western Atlantic Northeast Distant Waters to U.S. fishermen in 2001 (Watson et al. 2004). NMFS, with cooperation from the Blue Water Fishermen's Associated conducted a three year experiment with different hook types and sizes in the Northeast Distant Waters (Watson et al. 2004).

Loggerhead interaction with the longline fishery occurs when loggerheads actively pursue squid bait as a food source and end up swallowing a hook or become

hooked in the beak (Witzell and Cramer 1995). Swallowed hooks are the hardest to remove without surgical procedures and result in the highest mortality. Through experimentation, NMFS found that large (18/0) circle hooks reduce loggerhead interactions by 70-90% depending on the bait used (NMFS-SEFSC 2001). Large circle hooks not only reduce overall interaction, but also significantly lower the percent of hooks ingested. As a result, NMFS banned “J” hooks in the western Atlantic longline fisheries (NOAA 2004). However, these regulations only apply to U.S. fisherman. Other nations that fish in the NED (Northeast Distant waters) do not require any specialized gear to reduce sea turtle interactions with the longline fishery.

Population Dynamics and Modeling

An understanding of the population dynamics of a species is necessary for successful management. Mathematical modeling of populations allows researchers to test the effects of alternative management actions on a species of concern. The models can then be manipulated to reveal a population’s reaction to different perturbations and management actions. A population model’s output can only be as accurate as the input for the model. Input for demographic population models often includes data on the rates of births, deaths, population growth rate, emigration, and immigration for the population (Chaloupka and Musick 1997). However, emigration and immigration are often excluded from loggerhead demographic models because questions still remain as to the extent of mixing between the subpopulations. Information on loggerhead sea turtle life history is still incomplete, particularly regarding the length of each life stage, the age at sexual maturity, and the average life span. Therefore, population models for loggerhead sea

turtles require careful interpretation. While a model can project a population's response to management, it should be used predominantly for a qualitative interpretation of a population's behavior. An example would be in the regulation of take limits in the longline fishery. The take limit must be set at a number, but this number may be arbitrary in the absence of robust population estimation. Loggerhead sea turtle models have been adaptive by adding information as it becomes available.

Frazer (1986) was the first to model the loggerhead's life history, thus initiating quantitative sea turtle management. All nesting female loggerheads were tagged on Cumberland Island, Georgia for a 17-year period to determine female survival and fecundity. From his mark-recapture data and other accumulated data collected from US nesting beaches, Frazer created a 54x54 age class life table. Frazer estimated survival rates for the majority of ages because at that point little data had been collected on the survival of hatchlings and juveniles. While current models utilize more current information on juvenile survivability, the basic work on female survivability and fecundity are still drawn from Frazer's tagging study.

Crouse et al. (1987) modified Frazer's life history table to create a stage based, or Lefkovitch, matrix model (Lefkovitch 1965). The Lefkovitch matrix is a special case Leslie matrix, in which the duration of life stages can vary and an organism can remain in the same life stage for more than one time step. For each life stage in a Lefkovitch matrix, information on the reproductive output, the probability of surviving and maturing into the next stage, and the probability of surviving and remaining in the same stage are required. In order to compensate for uncertainty in Frazer's 54-age class model, Crouse et al. (1987) collapsed Frazer's (1983) data into seven stage classes. The model assumed

no density dependence and a 1:1 sex ratio, both of which are questioned by the newest data (Braun-McNeill et al. in review). Another drawback of the Lefkovitch matrix is that time lags are difficult to assess from stage-based models because a stage can represent multiple years of an organism's life. Sea turtles have a long juvenile period and late age at maturation which builds an automatic time lag into any model projections.

One of the first sea turtle projection models for management was created to determine the effect of TEDs on the population (Crowder et al. 1994). This model collapsed all adult/sexually mature turtles into one class, creating a five stage-class model. It predicted that there may be up to a 70-year time lag until recovery in the population is observed.

Information regarding the life history of loggerhead sea turtles has greatly increased since the Crowder et al. (1994) matrix model. Heppell et al. (2003) updated past matrix models with the new age-structure data from genetic, skeletochronology, and mark-recapture studies. A 36-age class model was used in order to better detect time lags, which can be obscured in stage-based models. It was the first model to break the adult life stage into breeders and non-breeders and include remigration intervals in the model structure. The model also updated stage class lengths and survival estimates where new data were available. However, many of the survival estimates are based upon Frazer's work on Little Cumberland Island, GA. More repetitive mark-recapture studies are needed to understand survival rates for all stage classes (Heppell et al. 2003).

Elasticity and sensitivity analyses are commonly conducted on matrix population models. An elasticity analysis gives the relative proportional changes for age/stage classes in relation to the proportional change in population growth, λ (deKroon 2000). It

can be argued that elasticities are the best indication of a matrix element's relative importance to population growth. Elasticity analysis for loggerhead sea turtle populations continually point to the large juvenile period as the most "important" life stage (Crouse et al. 1987, Crowder et al. 1994, Heppell et al. 2003). The word important here is a relative term, meaning that an increase in juvenile survivability results in the greatest increase in the population growth rate, λ , relative to increases in other model parameters. This is a commonly accepted tool to create management strategies and to determine the life stages management should focus on to best ensure population recovery.

The size and age class estimates for the above models come predominantly from two different methods. One method to determine the ages of turtles for the above models is length-frequency analysis, a common practice in fisheries to determine growth rates, age structure, and mortality rates (Westerheim and Ricker 1977). Length-frequency analysis is now used to model loggerhead sea turtle somatic growth, specifically to estimate size at the time of recruitment back to the northwestern Atlantic and size at sexual maturity (Bjorndal et al. 2000a, Bjorndal 2000b). Length-frequency analysis for loggerheads shows that growth is extremely variable, within and between age classes. Because some sea turtle models are based on size classes, this variability affects the size of a single class and accuracy in classifying turtles into the correct class.

A second technique for determining size classes for juveniles is with a long-term mark-recapture study. Data from a recent mark-recapture study indicate that loggerhead growth rates are extremely variable and takes an average of 17 years to grow 30cm SCL, from 50-80cm SCL (Braun-McNeill et al. *in review*). A length-frequency analysis using von Bertalanffy curves with stranded sea turtles predicts an average of 14 years for the

period of large juvenile growth from 50-80cm SCL (Bjorndal et al. 2001). The variability in the data will exist until there is a method to robustly determine age through either skeletochonology techniques or a long term mark-recapture study of juveniles is done with a large sample size over a long period of time.

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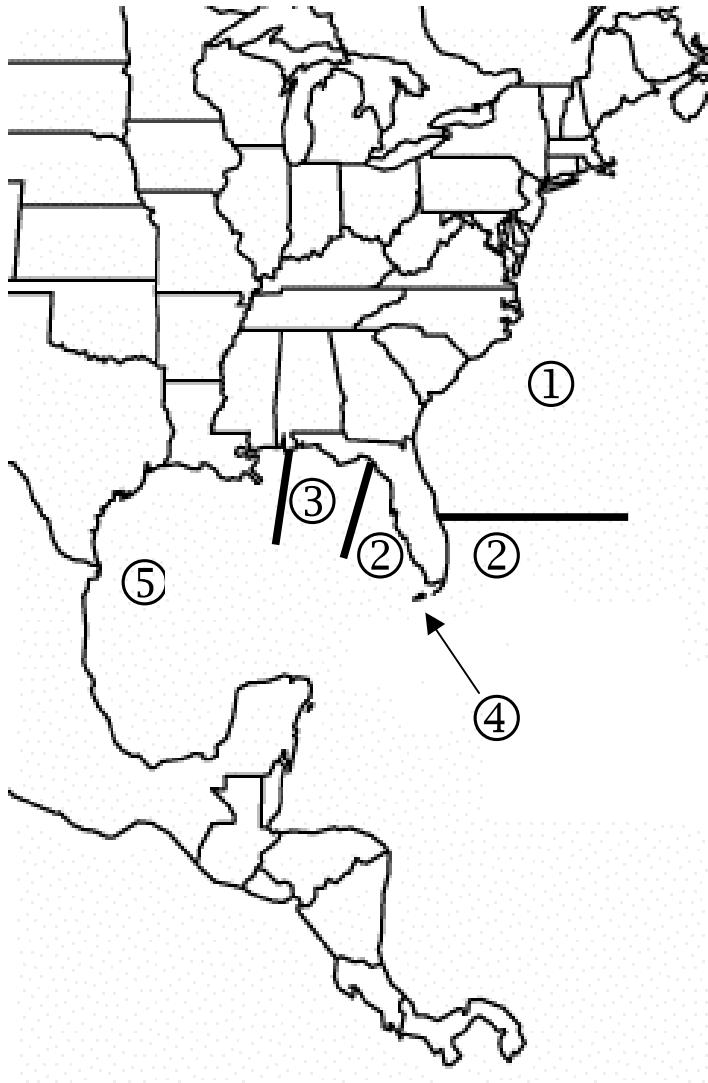
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Figure 1.1. Map the route of the post-hatchling trans-Atlantic migrations for the loggerhead sea turtle. The arrows indicate the current known as the North Atlantic Gyre.



Figure 1.2. Map of the recovery subpopulations of loggerhead sea turtles nesting along the coast of the eastern United States as defined by the Turtle Expert Working Group (TEWG 1998). All subpopulations are genetically distinct by matrilineal lines.



- (1) Northern nesting subpopulation (Hatteras, North Carolina to Cape Canaveral, Florida)
- (2) South Florida nesting subpopulation (Cape Canaveral to Naples, Florida)
- (3) Florida Panhandle nesting subpopulation (Eglin Air Force Base to Panama City, Florida)
- (4) Dry Tortugas nesting subpopulation
- (5) Yucatan peninsula nesting subpopulation (eastern Yucatan, Mexico)

CHAPTER 2 – ESTIMATION OF DEMOGRAPHIC PARAMETERS FOR LOGGERHEAD SEA TURTLES NESTING ON BALD HEAD ISLAND, NORTH CAROLINA

Abstract

Loggerhead sea turtle (*Caretta caretta*) mark-recapture data are difficult to model without violating assumptions of equal catchability because loggerheads exhibit reproductive skipping and imprecise site fidelity to nesting beaches. Loggerhead sea turtles are also difficult to study and only three estimates exist of annual adult survival in the literature. Multistate models offer a new approach to estimating life history parameters from mark-recapture data for loggerhead sea turtles. The multistate model incorporated reproductive skipping by creating an unobservable nonbreeder state and also accounted for transient individuals. This technique was applied to a nesting aggregation of loggerhead sea turtles on Bald Head Island, North Carolina, USA to obtain a more accurate estimate of survival rate for adult loggerheads than past models. I examined various factors that might influence sea turtle survival such as time, trap-dependence, and transience. The Akaike Information Criterion was used to rank the suite of models tested. The highest ranked model included a transient effect on survival, constrains the reproductive cycle to 4 years, and contained a time effect on recapture rates. This model estimated an annual survival rate of 0.853 for adult females. This is the first estimated adult survival rate in the literature for loggerhead sea turtles nesting in North Carolina. Fertility estimates and nest trends for loggerhead sea turtles nesting on Bald Head Island were also estimated. The components of fertility estimated were hatching success rate, clutch frequency, and remigration intervals. All of the estimates of fertility were consistent with those in the current literature.

Introduction

The loggerhead sea turtle (*Caretta caretta*) is a long-lived marine reptile that inhabits oceanic and coastal waters of the United States and nests on beaches along the

southeastern and Gulf coasts (TEWG 1998). The nesting population in the southeastern United States is divided into 5 genetically distinct matrilineal subpopulations (Bowen 1993, 1995). In the southeastern United States the breeding season extends from mid-April to mid-August. Females abandon the nest after egg deposition to lay multiple clutches during one breeding season. Individuals have been observed laying 1 - 7 clutches per season with an average of two weeks between nesting events (Limpus 1985, Miller et al. 2003). The number of years between observed nesting events ranges from 1 - 9 years, with an estimated average of 2.5 - 3 years (Dodd 1988, Schroeder et al. 2003). The fact that loggerhead turtles nest multiple times per season increases the probability of capturing each individual at least once during the nesting season. Even in a saturation tagging study, which has the goal of marking every nesting female, it is likely that not every nesting event is observed.

Loggerhead sea turtles are listed as globally endangered by the IUCN's Red List (MTRG 1996) and threatened in the United States under the Endangered Species Act (ESA). The ESA requires recovery plans for threatened species as well as population monitoring. To create an effective recovery plan there must be an understanding of the species' life history parameters and demographic structure. This information can then be incorporated into a population model that allows researchers to determine how best to increase the species population numbers and project how the population will likely respond to management actions. The most current population model for the loggerhead sea turtle investigated the effect of turtle excluder devices on population growth rate and juvenile survival rates (Crowder et al. 1994, Heppell et al. 2003). To successfully model

any population, life history parameters are needed as input for the model and data are often collected through mark-recapture studies.

Mark-recapture studies provide data necessary to calculate demographic rates including survival, emigration/immigration, and recapture probabilities, along with fecundity. Fecundity is not traditionally estimable from mark-recapture studies. However, fecundity of adult loggerheads is fairly easy to obtain because they are “captured” and marked only when they are coming up onto nesting beaches. Fecundity is based upon the number of nests/female/season, reproductive skipping, and eggs per clutch which are only obtainable by identifying individual females. While it is ideal to track multiple generations of individuals from birth to death, the sea turtle’s elongated juvenile stage and seasonal adult migrations do not allow for such studies (Lebreton et al. 1992). Sea turtles do present a unique case because the females must emerge from the ocean to lay their nests on sandy beaches. This creates a yearly window to conduct mark-recapture studies on the adult female portion of the population. Females also exhibit site fidelity to nesting beaches, which is beneficial for long term mark-capture studies (Bell and Richardson 1978, Limpus 1985, Schroeder et al. 2003).

Only three estimates exist for adult survival in loggerhead turtles nesting in the southeastern United States. Frazer (1983) first calculated survival rates for adult females using life history tables from a mark-recapture study on Little Cumberland Island, GA (Table 2.1). The other two estimates from Wassaw Island, GA and Melbourne Beach, FL were estimated from Cormack-Jolly-Seber (CJS) open population models (Cormack 1964, Jolly 1965, Seber 1965, TEWG 2002). However, a key assumption is violated when nesting female mark-recapture data are modeled in either a life table or CJS model.

In the traditional single-state model every marked individual present in the population at time (i) is assumed to have the same probability of recapture (p_i) at every sampling occasion.

Mark-recapture data for female loggerhead turtles tagged during the breeding season violate this assumption in a single-state model because loggerhead turtles exhibit variable reproductive skipping, during which time they are not available for capture on the nesting beach (Carr and Carr 1970, Carr et al. 1978). Reproductive skipping has been observed during long term saturation tagging programs across species and on multiple beaches around the world (Bell et al. 1978, Bjorndal et al. 1983, Hughes 1982, Limpus 1985). In years when a sea turtle is not reproductively active it is unobservable at the study site, resulting in heterogeneous capture probabilities among individuals (Prévot-Julliard et al. 1998). Kendall et al. (1997) defined this as nonrandom temporary emigration and it must be taken into account in model construction (Burnham 1993). An absence from the study site is nonrandom because a female's return to the study site as a breeder is dependent on her breeding status the previous year (Viallefont et al. 1995). However, the remigration interval is variable at the individual level. The violation of homogeneous capture probabilities in a single-state model will bias estimates of survival and recapture probabilities low (Kendall et al. 1997) and could lead to population models that do not accurately represent the true population. Female loggerheads may also survive to a potentially observable capture occasion, but nest on beaches outside the study site. Site fidelity for loggerhead turtles between nesting seasons average 5km with a range from 0 - 95km (Miller et al. 2003). A female may also switch between proximal nesting sites within a season, escaping capture. This results in some females that are

captured once on the study site and never recaptured. These individuals are known as transients in the population and will also bias survival and recapture estimates low if not accounted for in model structure (Prévot-Julliard et al. 1998).

A multistate mark-recapture model offers a framework that can incorporate these characteristics of the loggerhead sea turtle's nesting behavior by allowing individuals to move between states (Kendall 2004). Multistate model development has evolved and multiple states are no longer limited to geographic locations. States can be physiological (i.e. sex, weight, age), reproductive (i.e. breeder, nonbreeder), include live and dead recoveries, and also be completely unobservable (Nichols et al 1992, Nichols et al 1994). The key development in multistate models for the study of sea turtles is the ability to model unobservable states (Lebreton and Pradel 2002). Unobservable states can be any life stage or portion thereof for which detection probability at the study site is zero. Multistate models have been used to model unobservable seed/dormant states in plants (Kéry et al. 2005), breeding cycles in leatherback sea turtles (Rivalan et al. 2005) and fur seals (Beauplet et al. 2006), and reproductive costs in bird species (Doligez et al. 2002). Multistate models have not been used to model a loggerhead sea turtle population prior to this study.

The type of multistate model used to analyze nesting beach mark-recapture data is the Arnason-Schwarz model, which is dependent on the state to which an individual is moving (Brownie et al. 1993). The assumptions for the conditional Arnason-Schwarz multistate model include (Kendall 2004, Schwarz and Arnason 1996):

1. Each animal in state r at time i has the same probability of surviving to time $i+1$, of transitioning, given it survives, to any state s just before time $i+1$, and of being observed at time $i+1$, given that it is present.
2. Marks do not affect the survival or behavior of the animal, are not lost, and are recorded correctly.
3. Each animal is independent with respect to survival, transitions, and detection probability.
4. Each individual has the same probability of capture during every sampling period. (homogeneous capture assumption)
5. The state of each animal is assigned without error at each capture occasion.

In the case of loggerhead sea turtles, assumptions 1 and 4 are violated due to reproductive skipping. It is possible to release the homogeneous capture assumption by modeling trap-dependence (Pradel et al. 1994). When the assumption is released, individual animals are not required to have the same recapture probability in any given sampling period (Lancia et al. 1994, Pollock et al. 2002). The failure to recapture a female in a sampling period does not necessarily indicate death, permanent emigration, or completely random emigration as implied in single-state models (Kendall et al. 1997). However, just as in a CJS model, if an individual is captured only once, the multistate model cannot differentiate its absence between death and emigration. In the multistate models, the probabilities of moving from a nonbreeder to a breeder state are known as transition probabilities. These transition probabilities represent the remigration interval, or the number of years it takes for an individual to return to the breeder state. The only

estimates of remigration intervals in the literature are from the tagging study on Little Cumberland Island, GA (Frazer 1983). Frazer (1983) estimated the number of years skipped between observed reproductive events empirically, using a frequency distribution. Calculating the transition probabilities directly from the data introduces bias if these probabilities are then used to derive survival probabilities or included in a population model (Martin et al. 1995). In the case of loggerhead turtles, recapture probabilities are directly linked to the individual's breeding cycle. Calculating the survival and recapture probabilities independently from one another directly from the raw data introduces bias to the estimates because the two parameters are correlated (Viallefont et al. 1995). Estimates of recapture, survival, and transition probabilities are all outputs of the multistate model. Because all three parameters are estimated from the same multistate model, bias is reduced.

This study utilizes the model developed by Rivalan et al. (2005) to estimate demographic parameters for loggerhead sea turtles nesting in the northern subpopulation along the southeastern coast of the USA. A multistate model has not been previously applied to loggerhead sea turtle data and will provide estimates of survival, transition, and recapture probabilities without violation of key assumptions in the mark-recapture framework. This study will also provide updated demographic estimates for loggerhead sea turtles nesting in North Carolina.

Methods

Study Site

Fieldwork for this study was conducted through the Bald Head Island Conservancy on Bald Head Island, North Carolina USA. Bald Head Island, NC is the southernmost barrier island in North Carolina, located at the mouth of the Cape Fear River (Figure 2.1). The beaches monitored include those of the Village of Bald Head Island and also the Bald Head Island State Natural Area, managed by Fort Fisher State Recreation Area. There are approximately 15.3km of suitable nesting beaches for sea turtles, with the majority of nests laid on the ocean facing beaches. The availability of suitable nesting beach is affected by the natural erosion/accretion of barrier island beaches and erosion from a dredged shipping channel beginning approximately 20 feet offshore from the West facing beach.

Data Collection

Night patrols of the beach began in 1983 with an attempt to identify females within season through photo-identification. Photo-identification of females between seasons is not possible due to changes in epibiont patterns on the carapace. In 1991 the Bald Head Island Conservancy was granted permits to flipper tag nesting females. By identifying the majority of all females emerging from the ocean to nest, the study is referred to a saturation tagging project. Data for this study currently includes 16 years, from 1991-2006.

Each year for the first two weeks of the conventional nesting season (approximately May 15-May 29) the beaches were patrolled in the morning for sea turtle nests. The beaches were also only patrolled in the mornings after the peak of nesting

season, usually after August 15. Identification of individuals nesting during the weeks of morning-only patrols was not possible. During the eleven weeks of peak nesting season, the beaches were patrolled nightly using off-road vehicles from dusk to dawn (9pm to 6am). However, not every nesting event was observed due to vehicle failure, inability to traverse eroding beaches during high tides, and staff availability.

Two Inconel metal tags (National Band and Tag Co.), were applied to each female, one in the trailing edge of each front flipper. New flipper tags were applied for those females emerging with no tags and lost tags were replaced. Starting in the summer of 2002, females have also been tagged with passive integrated transponders (PIT tags), injected into the female's left shoulder. It is hoped that PIT tags will not migrate through tissue in the shoulder and last longer than flipper tags, increasing detection rates by decreasing tag loss.

Additional data collected for individual females included straight carapace length (SCL), straight carapace width (SCW), curved carapace length (CCL), curved carapace width (CCW), latitude and longitude of the nest collected by a global positioning systems (GPS) receiver, time of observation, and current flipper and PIT tag numbers. The straight carapace lengths were obtained using a set of calipers, while the curved lengths are measured with a flexible tape measure. Clutch size was only recorded at the time of nesting if the nest was relocated. Nests were only relocated if they are laid below the high tide line. Otherwise, an estimate of clutch size was made during the nest excavation, three days after the nest hatches. All available data on clutch sizes were used to calculate demographic parameters.

Parameters

The dataset from Bald Head Island has undergone limited demographic analysis, with two papers available in peer-reviewed literature. Webster and Cook (2001) discussed basic nesting statistics for the 1991 and 1992 nesting seasons and Hawkes et al. (2005) analyzed the dataset from 1991-2004, presenting descriptive statistics including basics on the nesting data and information on neophyte versus re-migrant nesting females. Life history parameters, such as number of eggs per clutch, hatching success, and nests/season/female, from Bald Head Island, NC had not been updated since Hawkes et al. (2005) nor compared to other long term studies in the southeastern USA.

As part of this study, the hard copy data have been thoroughly reviewed and corrected for errors found in tagging database. Hawkes et al. (2005) reported that from 1991-2003, 477 individual loggerhead turtles had been tagged. After review, a corrected number of 415 individuals had been tagged from the period 1991-2006. Hatching data were also reviewed and corrected.

Multistate Model

The data provided 16 years of mark-recapture data, for which a capture history was created for every tagged individual. The basic model followed that of a multistate conditional Arnason-Schwarz model in which survival and capture probabilities were separately identifiable (Schwarz and Arnason 1996, Lebreton et al. 1992).

The model structure for loggerhead sea turtles followed that developed in Rivalan et al. (2005) for leatherback sea turtles. The multistate model chosen allowed individuals to transition between two basic states, an observable breeder state and unobservable nonbreeder state. Individuals could also temporarily emigrate from the study site, during

the years in which they were nonbreeders (Fujiwara and Caswell 2002, Kendall and Nichols 2002, Pradel et al. 1997). The temporary emigration for this model was nonrandom, first order Markovian (Kendall et al. 1997). Individuals could spend multiple years in the state of nonbreeder. However, the maximum number of years in the nonbreeder state was constrained in the transition matrix depending on the length of the cycle being tested. In this case, the number of states was defined by the number of years skipped between reproductive events plus one as a breeder. The multistate model for unobservable states was composed of a transition matrix (ψ) with observable breeder states “B” and unobservable nonbreeder states “NB” and survival (S) and recapture (P) probabilities expressed as vectors (Nichols et al. 1994). The numerical subscripts for NB indicated the number of years skipped since last in the breeder state. The model below constrained the breeding cycle to two years, which allowed females to either breed in two consecutive years or skip one year between breeding events.

$$\begin{matrix} & B & NB \\ \begin{matrix} B \\ NB \end{matrix} & \begin{bmatrix} \psi^{B,B} & \psi^{B,NB_1} \\ \psi^{NB_1,B} & \psi^{NB,NB} \end{bmatrix}_t & \begin{bmatrix} S^B \\ S^{NB} \end{bmatrix}_t \begin{bmatrix} P^B \\ P^{NB} \end{bmatrix}_t \end{matrix} \quad (1)$$

Loggerheads have been observed skipping anywhere from 0 to 9 years between active breeding years (Dodd 1988; Limpus 1985). However, the average number of years between breeding events from beaches worldwide falls between 2.5 and 3.0 years (Miller et al. 2003). The transition matrix and survival and capture vectors were expanded based on the number of states. Individuals in the observable and unobservable states were assumed to have the same survival rates since data were not available for adult loggerhead females in the open ocean (Kendall 1994).

To estimate parameters in a transition matrix with unobservable states required the use of an identify link function (Choquet et al. 2005). When using the identity link function, estimates were allowed to fall outside the range [0, 1] (Cooch and White 2006). Transition probabilities in row 1 of Equation 2, element (1,2) were not estimable as the transition to the nonbreeder state was unobservable.

When the transition matrix in Equation (1) above was expanded to a breeding cycle of 4 years, it became:

$$\begin{array}{c}
 \begin{array}{c} B \\ NB_1 \\ NB_2 \\ NB_3 \end{array}
 \begin{array}{c} B \quad NB_1 \quad NB_2 \quad NB_3 \\ \left[\begin{array}{cccc} \psi^{B,B} & \psi^{B,NB_1} & \psi^{B,NB_2} & \psi^{B,NB_3} \\ \psi^{NB_1,B} & \psi^{NB_1,NB_1} & \psi^{NB_1,NB_2} & \psi^{NB_1,NB_3} \\ \psi^{NB_2,B} & \psi^{NB_2,NB_1} & \psi^{NB_2,NB_2} & \psi^{NB_2,NB_3} \\ \psi^{NB_3,B} & \psi^{NB_3,NB_1} & \psi^{NB_3,NB_2} & \psi^{NB_3,NB_3} \end{array} \right] \end{array}
 \end{array} \quad (2)$$

The only estimable nonbreeder probabilities were those which move an individual through the transition matrix. Transition probabilities of all other movements between nonbreeder states were not estimable in this model because only the transitions of movement to the breeder state were observable. The inestimable nonbreeder to nonbreeder transitions were constrained to 0, reducing the above matrix to:

$$\begin{array}{c}
 \begin{array}{c} B \\ NB_1 \\ NB_2 \\ NB_3 \end{array}
 \begin{array}{c} B \quad NB_1 \quad NB_2 \quad NB_3 \\ \left[\begin{array}{cccc} \psi^{B,B} & \psi^{B,NB_1} & 0 & 0 \\ \psi^{NB_1,B} & 0 & \psi^{NB_1,NB_2} & 0 \\ \psi^{NB_2,B} & 0 & 0 & \psi^{NB_2,NB_3} \\ \psi^{NB_3,B} & 0 & 0 & 0 \end{array} \right] \end{array}
 \end{array} \quad (3)$$

In each row of the transition matrix (for any breeding cycle length), only two transitions were estimable. Elements representing a transition to the breeder state (all elements in column 1 of Equation 3) were estimable because they could be observed.

However, all elements in the superdiagonal were not directly estimable because they were transitions to unobservable states. Therefore, all elements in the superdiagonal were estimated as complements to elements in column 1. The equation for a 4-year breeding cycle became

$$\begin{array}{c}
 B \\
 NB_1 \\
 NB_2 \\
 NB_3
 \end{array}
 \begin{array}{c}
 B \quad NB_1 \quad NB_2 \quad NB_3 \\
 \left[\begin{array}{cccc}
 \psi^{B,B} & 1 - \psi^{B,B} & 0 & 0 \\
 \psi^{NB_1,B} & 0 & 1 - \psi^{NB_1,B} & 0 \\
 \psi^{NB_2,B} & 0 & 0 & 1 - \psi^{NB_2,B} \\
 1 & 0 & 0 & 0
 \end{array} \right]
 \begin{bmatrix} S \\ S \\ S \\ S \end{bmatrix}_t
 \begin{bmatrix} P \\ 0 \\ 0 \\ 0 \end{bmatrix}_t
 \end{array}
 \quad (4)$$

with a matrix of breeding transition probabilities, a vector of survival rates, and a vector of recapture probabilities.

Time dependence (year-to-year variation) was not tested on the matrix of transition probabilities due to the unrealistic number of parameters it would have added to the model. The data were sparse and convergence issues would arise in a model with many more parameters (Philippe Rivalan pers. comm.). The estimates of survival, recapture, and breeding transitions were estimated using maximum likelihood methods and if the model cannot estimate the local minima for each estimate, the model would not converge and the estimates and their associated standard deviations would be biased. In Equation 3 the reproductive cycle was constrained to 4 years, forcing a nonbreeder of 3 years, ψ^{NB_3B} , to breed the next year. This element (4,1) in the matrix was therefore equal to 1. Elements 2-4 in the capture vectors were constrained to 0 due to the impossibility of capturing individuals in the unobservable states. Recapture probabilities must be estimated from the model and not the raw data when the capture rate is less than 1.0, such

was the case with these data (Pollock et al. 1990, Martin et al. 1995). Estimates of recapture, transition and survival were all separately identifiable. Using the multistate model to estimate all three parameters reduced the bias in survival and transition estimates, the two estimates which have high biological value. However, the estimates were still biased low due to the sparse data and high number of transients. In this study program MSURGE was used to test a suite of *apriori* models that estimated recapture, transition, and survival probabilities (Choquet et al. 2005a).

Apriori hypotheses for the effects expected in the breeding cycle and survival parameters were made by examining the raw data and the knowledge of biology of loggerhead sea turtles. The models tested ranged from a breeding cycle of 2 to 5 year, which represent the suite of observed remigration intervals seen in the raw data. Given the distribution of observed remigration intervals in Figure 2.7, it's hypothesized that a model constraining the breeding cycle to either 3 or 4 years should emerge in the top models. A model with a transient effect on survival should also provide the best estimate of survival due to the high number of transients in the data. The estimation of survival without a transient effect will significantly bias the estimate low.

Goodness-of-fit Test

I used goodness-of-fit (GOF) to assess the model's fit to the data and indicated whether the chosen model was appropriate to use (Lebreton et al. 1992). However, no GOF test exists for a multistate model with unobservable states. As in Rivalan et al. (2005) the fit of the loggerhead data to a multistate model was tested with a modified single state GOF test. The single state GOF test was suitable because the one observable

state, breeder, acted as the single state (Rivalan et al. 2005). The single state GOF was the sum of two main test components, Test3 and Test2 (Lebreton et al. 1992).

Test3 is composed of two subtests, 3.SR and 3.SM. Test 3.SR detected if newly marked individuals had the same probably of recapture in successive years as those individuals marked in previous years, i.e. detection of transients. Test 3.SM tested whether the time elapsed from mark to first recapture was different for newly and previously marked individuals.

Test2 is composed of subtests 2.CL and 2.CT. Test 2.CL tested for a difference in expected time of next capture for individuals encountered and not encountered at time i , conditional on presence at both i and $i+2$. Component 2.CT tested whether the probability of capture at time $i-1$ is dependent on probability of capture at time i , also interpreted as immediate trap-dependence (Pradel 1993). Test 2.CT also detected non-random temporary emigration, or first order Markovian, which required the data to be modeled in a multistate framework (Pradel et al. 1997, Kendall et al. 1997, Schaub et al. 2004).

Tests for GOF components were executed in program U-CARE (Choquet et al. 2005). If tests for trap-dependence and transients tested significant, a revised GOF test was needed. The revised GOF took into account trap-dependence (Pradel 1993), transients (Pradel et al. 1997, Prevot-Julliard et al. 1998), and reproductive skipping (Viallefont et al. 1995). The revised GOF, accounting for these factors became (Rivalan et al. 2005):

$$GOF_m = \chi^2_{total} - \chi^2_{test2.CT} - \chi^2_{test3.SR} - \Delta dev$$

with

(5)

$$df_m = df_{\text{total}} - df_{\text{test2.CT}} - df_{\text{test3.SR}} - 1 .$$

Reproductive skipping was accounted for by calculating Δdev , defined as the difference in deviances for the most general model that incorporated reproductive skipping [$S_{t*\tau}$, $\psi_{\text{cycle} = 2}$, P_{t*m}] and the single state model that did not [$S_{t*\tau}$, P_{t*m}], calculated in MSURGE (Choquet et al. 2005a). The subscript t represents a time (year) effect, τ indicates the transience effect, and m represents the trap-dependence effect. In the model notation, transition was denoted as ψ with subscript $\text{cycle} = x$, in which the reproductive cycle was constrained to x years.

To correctly transform the data to reflect the results from the single state GOF, the data were pooled into two groups to account for trap-dependence. Pooling the data allowed individuals to have differing capture probabilities (Pradel 1993). The first group represented capture probability from first capture to first recapture. The second group represented capture probability from first recapture to all subsequent recaptures. The pooled data were used as the input file in program MSURGE and could be manipulated as age classes.

Transients were accounted for by specifying two artificial groups in MSURGE. Group one signified all individuals marked and never recaptured. Group two represented individuals that had been recaptured in at least once subsequent to the year of first capture. With these modifications the model included correction factors for both transients and trap-dependence, releasing the violation of any assumptions.

The candidate models selected to test were parameterized by varying effects on survival and capture probabilities and changing the length of the breeding cycle.

Each combination of models was tested with the breeding cycle constrained to 2, 3, 4, and 5 years ($\Psi_{\text{cycle}} = 2, \Psi_{\text{cycle}} = 3, \Psi_{\text{cycle}} = 4, \Psi_{\text{cycle}} = 5$).

Survival models included time dependence (S_t) transients (S_τ) interaction between time dependence and transients ($S_{t*\tau}$) and additive effects of time dependence and transients ($S_{t+\tau}$). The possible effects on capture included time dependence (P_t) interaction between time dependent and trap-dependence (P_{t*m}) and time dependent with additive trap-dependence (P_{t+m}). Models were fitted in program MSURGE (Choquet et al. 2005a). MSURGE calculated parameters using maximum likelihood estimation (MLE). No models were tested with only a trap-dependence effect on recapture because of the variability in sampling effort between seasons over the 16 year period. The variability in sampling effort over the 16 year study period is another reason the estimates would be biased low.

Model Selection

Model selection was based on lowest QAIC values and biological relevance (Akaike 1974, Lebreton et al. 1992).

$$\text{QAIC} = 2 \times np + \left(\frac{\text{deviance}}{\hat{c}} \right) \quad (6)$$

The variance inflation factor, \hat{c} , identified overdispersion in the data and was calculated from the GOF as, $\text{GOF}_m / \text{df}_m$ (Burnham et al. 1987, Lebreton et al. 1992). If overdispersion were to exist in the data, models were ranked based on quasi-likelihood AIC, QAIC. The standard deviation of parameter estimates were also corrected by the variance inflation factoring MSURGE.

The ΔQAIC values, calculated as

$$\Delta\text{QAIC} = \text{QAIC}_i - \text{QAIC}_{\min}, \quad (7)$$

were used to analyze the relative support of the data for each model in relation to the model with the lowest QAIC (Burnham and Anderson 1998). The ‘rule of thumb’ suggests that all models with a ΔQAIC value less than 2 have equal weight in the data and must all be considered (Cooch & White 2006). A value between 2 and 7 suggests there is some support in the data for the model. Any value greater than 7 suggests no support in the data for the model.

To further determine the support for each of the models, Akaike weights were calculated, using QAIC values (Buckland et al. 1997, Burnham and Anderson 2002). Akaike weights originate from Akaike’s model likelihood theory that the likelihood of the model(M) given the data(x), written as $\mathcal{L}(M_i | \underline{x})$, is proportional to $\exp(-\frac{1}{2} \Delta_i)$ (Akaike 1983). The Δ_i values are equal to the differences in model AIC or QAIC values. This proportional equation could then be used to calculate normalized model weights, w_i , for any model i in a set of R models (Anderson and Burnham 1999).

$$w_i = \frac{\exp(-\frac{1}{2} \Delta_i)}{\sum_{r=1}^R \exp(-\frac{1}{2} \Delta_r)} \quad (8)$$

The model weight is a relative index for model i ’s likelihood against any other model in the set. As a ‘rule of thumb.’ if a model’s Akaike weight is greater than or equal to 0.9 the model can be considered to contain the best predictors of the data (Burnham and

Anderson 1998). Ratios of model likelihoods, w_i/w_j , give a relative index for the strength of one model to another. For instance, if the ratio of w_i/w_j is 5, model i is 5 times a more likely model, given the data, than model j .

The proportion of transients in the data was calculated based on the survival rates estimated by the model

$$\text{Proportion of transients} = 1 - \frac{\phi_{a_1}}{\phi_{a_2}} \quad (9)$$

and provided an unbiased estimate to the proportion of individuals never recaptured (Pradel et al. 1997).

Results

Basic Demographic Statistics

Annual nest numbers for loggerheads nesting on Bald Head Island are found in Figure 2.2. From 1980-1991 the data included total nest numbers, with no ability to discern between loggerhead and green sea turtle (*Chelonia mydas*) nests. The data from 1992 to 2006 represented only loggerhead nests. However, the number of green sea turtle nests laid on Bald Head Island was insignificant and the linear regression of nests laid over time was from 1980-1991. The linear regression of the number of nests laid per year indicated a weak, but significant negative trend through time ($R^2 = 0.29$, $F_{1,25} = 10.21$, $P = 0.00038$).

During the study period from 1991 to 2006, 415 female loggerheads were identified and tagged. Females captured with tag scars were retagged and assigned a new unique identification number. The inability to identify females that have lost tags could

result in individuals with multiple identification numbers. Only 67 of the 415 marked individuals were recaptured at least once subsequent to the year in which first marked (Figure 2.3). Loggerheads recaptured in years succeeding the year of first capture will be referred to as remigrants. The other 348 individuals were only observed at the study site during the year of first capture and will be referred to as transients.

The estimate of the minimum number of females nesting yearly was correlated with the number of observed nests laid per year, with a correlation of 0.93. The number of remigrants versus first captured females indicated no visible trend (Figure 2.3). In 2005 only 10% of identified females were remigrants whereas in 2006, 54% of all identified females were remigrants.

While this study was considered a saturation tagging study, all emergences of females from the ocean were not observed. Over the 16 year period, the average proportion of observed emergences that resulted in a successful nesting was 0.79 (range 0.66 - 0.90). This was not an estimate of the proportion of females identified from emergences due to possible multiple emergences by one female within a single breeding season.

The observed number of nests laid during a reproductive season ranged from 1 to 6, with a mean of 2.09 nests/season/female. This mean was biased low because the majority of females were observed nesting only once in a reproductive season in this study (Table 2.2, Figure 2.4). The mean interval between nesting events was 16.5 days, with a range of 5 to 64 days. These were observed nesting events, in which it was expected nesting events were missed for females with nesting intervals in the higher range (Mortimer and Carr 1987). Three observed nesting intervals were at the low range

(<10 days), but were correct according to the raw data, in which it may be possible flipper tag numbers were transposed. Therefore, the median, 14 days, better represents the data and reproductive biology of the loggerhead sea turtle.

The average number of eggs laid per clutch was 118 with a range of 39-184 (Table 2.2). The “corrected” average hatching success rate for all nests with reported rates >0.0 was 0.786. Nests that were destroyed before hatching or lost to hurricane or erosion were not included in the hatching success analysis (VanBuskirk and Crowder 1994). The median for hatching success rate is 0.875, which better represented the hatching success of successful nests (Figure 2.5). Many of the nests with lower reported hatching success rates most likely suffered from egg or hatching loss. The average of all nests (N=1228), including those which failed to hatch, was 0.63, with a median of 0.83.

Multistate Model

The GOF test indicated a lack of fit of the data to the global model (S_{τ^*t} , P_{t^*m}). The tests for components 3.SR, 2.CT, and 2.CL of the GOF were all significant indicating transients and trap-dependence in the data (Table 2.3). In this study trap-dependence can be biologically interpreted as non-random temporary emigration from the study site. (Choquet et al. 2005). It is known that individual animals are not likely to been present on the study site in two consecutive years (reproductive skipping) and are temporarily emigrating from the nesting beach in a non-random pattern. While test component 2.CL was found significant there is neither a simple interpretation for the test’s meaning to a method account for the lack of the test’s fit in the overall GOF (Choquet et al. 2005). The overdispersion coefficient, \hat{c} , calculated from this dataset was

1.5638 and was input in MSURGE for adjustment of standard deviations around estimates and QAIC values.

Of the 48 total models tested, five models were chosen for further analysis. I considered the top five models to be those that had the lowest QAIC values (Table 2.4). All top five models had a transient effect on survival, breeding cycles ranging from 3-5 years, and a time effect on recapture. Three of the top five models also had an additive trap-dependence effect on recapture. The top four models based on lowest QAIC all had ΔQAIC values of 2 or less and model 5 had a ΔQAIC value of 4. This indicated very little support in the data for differences between the five models. All of the top five models also had between 20 – 22 identifiable parameters. With these similarities it was difficult to differentiate between the top five models based on the QAIC values.

The model with the lowest QAIC modeled a transient effect on survival, constrained the breeding interval to 4 years, and modeled a time effect on recapture, $[S_\tau, \psi_{\text{cycle}=4}, P_t]$, further referred to as Model 1. Model 1 had a total of 5760 parameters, but only 20 of those were estimable. The model estimated two parameters for survival, three for the breeding transitions, and 15 recapture parameters. The model with the second lowest QAIC value modeled a transient effect on survival, constrained the breeding interval to 3 years, and an additive effect of time and trap-dependency on recapture, $[S_\tau, \psi_{\text{cycle}=3}, P_{t+m}]$, hereafter referred to as Model 2. Models $[S_\tau, \psi_{\text{cycle}=4}, P_{t+m}]$ (Model 3) and $[S_\tau, \psi_{\text{cycle}=5}, P_t]$ (Model 4) had the same model deviances, have a ΔQAIC of 2, and contained 21 identifiable parameters. The only difference between the two models was that when the breeding cycle is increased to 5 years, trap-dependency no longer had an effect on recapture.

Model 1 estimated the survival rates for age group one (individuals never recaptured) to be 0.281 (CI: 0.187, 0.374) and for age group two (individuals recaptured at least once) as 0.853 (CI: 0.781, 0.925) (Table 2.5). The point estimates of survival rates for both age classes were the same for the top five models, except for Model 2. The survival rates for Model 2 for age classes one and two were 0.276 (CI: 0.184, 0.367) and 0.830 (CI: 0.7611, 0.900), respectively.

Transition probability estimates for the top five models were again the same for Models 1, 3, 4 and 5 (Table 2.5). Models 4 and 5, which constrained the breeding cycle to 5 years, estimated transition from state NB_4B to B,B at 1.0 indicating that all females had bred after 3 years as a nonbreeder even though the model allowed them to remain as nonbreeders for 4 years.

Recapture probabilities for Model 1 ranged from 0.195 to 0.899, discounting parameters that reached a boundary of either 0 or 1. Four of the recapture probabilities estimated reached the boundary parameter of 1, indicating a lack of fit in the data. This was most likely a result of the sparse data, with the majority of turtles having no recaptures. The boundary parameter of 0 estimated for 1992 resulted because no turtles were recaptured from 1991 (the first year of tagging) during this year. The low estimate of 0.195 for 2005 was a result of there being very few recaptures this year, and none of the females first captured in 2004 re-nested in 2005.

The model weights and relative likelihoods lent little to the differentiation of the top five models (Table 2.7). The model weight for Model 1 was only 0.39 and weights decreased for subsequent models. This indicated that no one model contained the parameters that best described the data. Table 2.8 contained the ratio of model weights

for each pair of models, given as the row divided by the column. Model 1 was less than two times more likely to be a better model than Model 2, and provided little strength for choosing one over the other. However, Model 1 was 7.39 times better than model 5, which indicated support for selecting Model 1 over Model 5. However, the evidence for choosing Model 1 over 2, 3, or 4 was not strong by model deviance, ΔQAIC , or QAIC weights. Therefore, the estimates for each of the models 1-4 should all be considered with equal likelihood.

Discussion

The number of loggerhead nests observed on Bald Head Island has been decreasing during the years 1980-2006. While Bald Head Island actively protects sea turtle nests and has ordinances against beach front lighting and beach furniture, the loss of beach due to erosion most likely negates some of these efforts. The proximity of the dredged shipping channel to the beach as well as the installation of 16 geotextile sand tubes in 2005 along the western half of South Beach reduced the length of suitable nesting beach for sea turtles. Bald Head Island experienced unusually low loggerhead nest numbers in 2004, a phenomenon noted on all nesting beaches in the southeastern USA (M. Godfrey pers. comm.). No explanation for this one-year phenomenon exists. Nest numbers in 2005 and 2006 returned to similar numbers in the years before 2004.

The fecundity of adult females calculated from identified females nesting on Bald Head Island is similar to that from other beaches in the southeastern USA (Miller et al. 2003). Examination of the raw data reveals high variability in the reproductive cycle at an individual level. Very few individuals have the same observed remigration interval

over their entire tagging history. Evidence suggests sea surface temperature, feeding ground conditions or other environmental variation may drive the length of a female's reproductive cycle (Carr and Carr 1970a, Hays 2000, Solow et al. 2002).

While the multistate model reduces bias in parameter estimates, there are still constraints to data collection that introduce bias. Mark-recapture studies for sea turtles are often limited by time and space. A time series of data spanning decades is ideal for a long-lived species such as sea turtles, but is not yet available. Space also becomes an issue due to political boundaries of beach surveys, which affects recapture estimates. Loggerheads may exhibit site fidelity to a degree that it is merely outside marked political and sampling boundaries. The estimates from the multistate model should be taken as conservative estimates, especially for survival. Another consideration when interpreting results should be the high proportion of transients in the data. The calculated proportion of transients in the sampled population is 67%, a very high proportion (Pradel et al. 1997). The model structure accounts for these individuals, estimating a more realistic survival rate.

Kendall et al. (2004) suggested sampling a buffer adjacent to the study site to detect those individuals nesting both within the study site and directly outside. Only individuals carrying tags from within the study site would be included in the data. During the 2005 nesting season the neighboring beach, Ft. Fisher State Recreation Area, was monitored in addition to Bald Head Island. Females previously tagged on Bald Head Island were detected nesting on both sides of the political boundary between Bald Head Island and Ft. Fisher within the 2005 breeding season. This acted as an experimental year and data from Ft. Fisher in 2005 were not included in the analyses because Ft. Fisher

was not monitored in any other years. However, cost and time required to monitor the extra 8.9km of beach proved insufficient. Turtles tagged while nesting on Bald Head Island have been observed nesting in subsequent years on other beaches in North Carolina (Hammock Beach State Park & Camp LeJeune Marine Corps Base) and as far south as Brevard County in Florida (Bald Head Island Conservancy unpub. data). Site fidelity will always be an issue in model development for sea turtles. Turtles may survive and be sighted on beaches outside the nesting site, but inclusion of this data to a model is not yet available.

Model Selection

A time (year) effect on recapture appeared in all five top models, in which some years had inestimable recapture rates (estimated by MSURGE at the boundary) due to the sparse data. I did not expect to see a cycle in recapture rates because all females that are recaptured exhibit differing breeding cycles beginning in different years. Therefore, the recapture rates estimated here should be interpreted with caution and are not of high biological value.

All five top models constrain the breeding cycle from 3-5 years, but there is support that Model 2 is not as biologically reasonable as the other top four models. Loggerhead turtles exhibit individual variation in the reproductive cycle and it is possible that the breeding cycle for some turtles is potentially longer than 5 years. However, the majority of turtles are observed skipping 0 – 3 years (Table 2.9, Figure 2.7). There is a high probability that females observed skipping 4+ years between nesting events on Bald

Head Island nested undetected within the study site or on a beach outside the study site. These assumptions cannot be confirmed from the data collected.

Model 2 constrains the breeding cycle to three years and estimates the probability of surviving and breeding in two consecutive years at 22% (Table 5). The estimate produced from Model 1 of 3% is more reasonable given our knowledge of reproductive skipping and is similar to other estimates for loggerheads (Frazer 1983, Carr 1970, Hughes 1982). The estimate from Model 1 is also consistent with inter-nesting patterns in the raw data. In the raw data there are 11 instances when females were observed as having a breeding interval of 4 years, skipping 3 years between breeding events. While it is possible that these females have an actual breeding interval of less than 4 years due to the detection probability of less than 1.0, it is unlikely. An estimate calculated from the raw data, while biased, indicates females only have a 4% probability of breeding in two consecutive years. Both frequency and cumulative distributions calculated from the raw data indicate that while most females breed after spending two years as a nonbreeder, there is a possibility of skipping 3 years (Table 2.9). Therefore, considering the support of the data for the models tested, restraining the breeding cycle to 3 years in the model does not represent the most likely behavior of individuals. Model 2 does not accurately represent the pattern of reproductive skipping observed in the wild.

Model 2 also estimates a lower survival rate than the other top five models, a possible effect of constraining the breeding cycle to three years. If some females truly have a reproductive cycle of 4 years, constraining the breeding cycle to three years in the model will lower the survival rate by failing to recognize females alive and present after skipping 3 years of breeding. This will also bias the recapture rates low.

In three of the top five models the additive effect of time and trap-dependence appear in recapture probabilities. The trap-dependence represents the temporary emigration from the study site and may indicate what we already know, that returning to the study site as a breeder is dependent on time spent as a nonbreeder. This factor is accounted for in the transition matrix. The effect of trap-dependence on recapture probability does not appear to affect any of the point estimates, as all of the estimates for Models 1, 3, 4, and 5 are the same. Biologically, this means there is no difference in the recapture rates between either capture and first recapture or between first recapture and any other recaptures. Model averaging will not improve the model selection since the point estimates for four of the top five models are the same.

According to the principle of parsimony, the model with the fewest number of parameters should be chosen over other top models as long as it is considered biologically reasonable (Burnham and Anderson 2002). Therefore, Model 1 can reasonably be selected over Models 3-5 since Model 2 was discarded as biologically unreasonable.

Annual Survival Probabilities

The ability to model trap-dependence, transients, and reproductive skipping in a multistate model with unobservable states is an extremely valuable advance in population modeling. The estimates produced from this model are improved over past models by applying new methods to prevent violation of key assumptions and modeling key biological characteristics (Perret et al. 2003). The survival estimates produced from four of the top five models ($\Phi_{a2} = 0.8530$) are higher than other survival estimates calculated

from other nesting beach mark-recapture studies (Table 3.1). The most recent estimates calculated by TEWG (2000) do not account for reproductive skipping or transients, which may be the cause for lower estimates. The survival estimate calculated in this study may also be higher because the majority of data are after the implementation of TEDs in 1992. The original TED design was estimated to decrease bycatch of loggerhead sea turtles in trawls by 97% (Henwood et al. 1992).

Annual adult survival estimates for loggerhead sea turtles estimated from in-water studies are also higher than all estimates from nesting beach surveys. Both in-water studies of adults were conducted in Australia, on the southern Great Barrier Reef (sGBR) ($\Phi = 0.875$) (Chaloupka & Limpus 2002) and Heron Reef ($\Phi=0.9102$) (Heppell et al. 1996). However, these estimates are not directly comparable to estimates from nesting beach surveys as no in-water surveys have been conducted in the northwestern Atlantic specifically for adult loggerhead turtles. There have been aerial surveys and in-water tagging studies that have tagged adult loggerheads in the waters off the coast of the southeastern United States. Any comparison of adult survival is not appropriate between loggerheads in Australian waters and loggerheads in the western North Atlantic. Loggerheads in the Atlantic and Pacific Ocean basins are genetically distinct, affected by historically different fishing and harvest pressures, and benefit from different conservation measures.

The estimates from these in-water surveys around Australia are more similar to survival estimates for other long-lived marine species. The survival rate of adult nesting leatherback sea turtles was recently estimated at 0.91 (Rivalan et al. 2005). Adult survival estimates for other long-lived marine species such as humpback whales

(Mizroch et al. 2004), seabirds (Sandvik et al. 2005), and Florida manatees (Langtimm et al. 1998) typically have adult survival rates estimated at 0.90 or above. Techniques for analyzing mark-recapture data are continuously improving and allow for more appropriate modeling and assumptions. Survival estimates produced by these models are incorporated into population models, in which adult survival for long-lived species can often affect 10+ years in an individual's lifespan. Sensitivity analyses have shown population growth rates are also highly sensitive to changes in adult survival rates for long-lived species (Lebreton and Clobert 1991). Analyses of the possible effects of alternative management actions will be affected if the estimated apparent survival rates do not represent the true survival rates. While it is impossible to model true survival, the survival estimate from the multistate model should be incorporated into population projections because of its ability to incorporate reproductive skipping and transients into the model structure and hence give more accurate survival estimates.

One downfall of the data from Bald Head Island is the lack of consistent and accurate records of tag loss. Records of tag loss would allow us to classify unmarked females as either neophyte nesters or remigrant nesters with tag scars. Frazer (1983) accounted for tag loss by back calculating nesting histories for loggerheads returning to nest with tag scars. However, the nesting probabilities were directly estimated from the data and no account was made for transient behavior or capture of a turtle with lost tags originating from another nesting beach.

The mark-recapture study on Bald Head Island will continue into the future, which allows the multistate model to be updated yearly. To improve the quality of the data we recommend that sampling methods should be revised to increase the interception

rate of nesting females. Our suggestions include caging the nests after dawn, increasing the number of patrol vehicles, and possibly walking the beach when tides do not allow the entire beach to be traversed by vehicle. Caging the nests at dawn would allow for patrols to continue after a female has been identified, instead of waiting at the site for her to return to the ocean to cage the nest. The continued use of PIT tags should also decrease tag loss and increase the ability to identify females that have lost their external flipper tags. All possible improvements should be made to data collection as this mark-recapture study provides critical information on the northern subpopulation of loggerhead turtles.

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Table 2.1. Published annual survival rates for adult loggerhead sea turtles

Survival Rate	Method type	Survey type	Location	Source
0.875	Cormack-Jolly-Seber model	in-water	Great Barrier Reef, Australia	Chaloupka & Limpus 2002
0.9102	Cormack-Jolly-Seber model	in-water	Heron Reef, Australia	Heppell et al. 1996
0.8091	life table	nesting beach	Little Cumberland Island, GA USA	Frazer 1983
0.782	Cormack-Jolly-Seber model	nesting beach	Mon Repos, Australia	Heppell et al. 1996
0.79	Cormack-Jolly-Seber model	nesting beach	Wassaw Island, GA USA	NMFS-SEFSC 2001
0.83	Cormack-Jolly-Seber model	nesting beach	Melbourne Beach, FL USA	NMFS-SEFSC 2001

Table 2.2. Estimates of fertility parameters for marked loggerhead sea turtles nesting on Bald Head Island, North Carolina from 1991-2006.

Parameter	Estimate	Range	Median	Mode	Standard Error	Number of Observations
Nests / season / female	2.09	1 - 6	2	1	0.058	505 (415 females)
Eggs per nest	119	39 - 184	120	116	0.071	997
Hatching success rate	0.786	0.007 - 1.0	.875	0.923	0.007	984

Table 2.3. Components of the goodness-of-fit test for the multistate model. a) components of GOF test with final calculation, b) delta deviation calculation.

a. Components of Goodness-of-fit test			
Test component	χ^2	P-value	df
3.SR	65.76	1.98E-09	12
3.SM	4.80	0.90	10
2.CT	53.85	6.49E-07	13
2.CL	31.66	4.47E-03	14
Total	156.07		49
GOF _m	35.97		23
		\hat{c}	1.56377

b. Δ dev Calculation		
Model	Deviance	
Single state S(τ .t), P(t.m)	782.019	
Multistate S(τ .t), cycle2, P(t.m)	781.519	
Difference	0.499	

Table 2.4. Quasi-likelihood Akaike Information Criteria (QAIC) values for all 48 models with the number of identifiable parameters in parentheses. The models in bold represent the 5 models with the lowest QAIC values.

Capture probability model	Survival probability model			
	S_{t^*t}	S_t	S_t	S_{t+t}
Breeding cycle constrained to 2 years				
P_t	634.22 (46)	606.32 (18)	651.75 (31)	633.14 (60)
P_{t+m}	600.86 (47)	575.87 (19)	622.93 (32)	599.90 (47)
P_{t^*m}	618.08 (60)	587.63 (32)	633.21 (45)	615.77 (60)
Breeding cycle constrained to 3 years				
P_t	591.21 (47)	562.26 (19)	607.70 (32)	590.45 (47)
P_{t+m}	582.75 (48)	555.32 (20)	602.42 (33)	583.88 (48)
P_{t^*m}	602.58 (61)	571.20 (33)	616.44 (46)	600.70 (61)
Breeding cycle constrained to 4 years				
P_t	585.34 (48)	554.60 (20)	599.76 (33)	584.72 (48)
P_{t+m}	584.75 (49)	556.60 (21)	602.34 (34)	585.88 (49)
P_{t^*m}	604.58 (62)	573.22 (34)	618.76 (47)	602.70 (62)
Breeding cycle constrained to 5 years				
P_t	587.34 (49)	556.60 (21)	601.76 (34)	586.72 (49)
P_{t+m}	586.75 (50)	558.60 (22)	604.34 (35)	587.88 (50)
P_{t^*m}	606.58 (63)	575.22 (35)	620.76 (48)	604.70 (63)

Parameters: P = capture probability, S = Survival probability. Subscripts: t = time, τ = transients, m = trap-dependence; + indicates additive effects, * indicates interaction effects

Table 2.5. Estimates of survival for age group two (individuals recaptured at least once) from the multistate model. Estimates are shown for the top 5 ranked models, with the lower (CI-) and upper (CI+) 95% confidence interval and standard deviation.

Model Description		Survival Estimate	CI-	CI+	SD
Model 1	S(τ) cycle4 P(t)	0.8530	0.781	0.925	0.037
Model 2	S(τ) cycle3 P(t+m)	0.8303	0.761	0.900	0.035
Model 3	S(τ) cycle4 P(t+m)	0.8530	0.778	0.928	0.038
Model 4	S(τ) cycle5 P(t)	0.8530	0.781	0.925	0.037
Model 5	S(τ) cycle5 P(t+m)	0.8530	0.778	0.928	0.038

Parameters: P = capture probability, S = Survival probability, cycle_x = breeding cycle constrained to x years.
Subscripts: t = time, τ = transients, m = trap-dependence; + = additive effects, * = interaction effects.

Table 2.6. Breeding transition probabilities estimated from the multistate model for the top models 1-5. Estimates constrained to 1.0 are not shown. The transitions are interpreted as the probabilities of moving from a state to another. Example: $B \rightarrow B$, probability of moving from a breeder state to the breeder state (breeding in two consecutive years).

Transition	Estimate	CI-	CI+	Estimate	CI-	CI+	Estimate	CI-	CI+
	Model 1			Model 2			Model 3		
$B \rightarrow B$	0.03	-0.02	0.09	0.22	-0.02	0.45	0.03	-0.04	0.11
$NB_1, B \rightarrow B$	0.31	0.20	0.43	0.34	0.19	0.49	0.31	0.20	0.43
$NB_2, B \rightarrow B$	0.81	0.66	0.96				0.81	0.65	0.97
	Model 4			Model 5					
$B \rightarrow B$	0.03	-0.02	0.09	0.03	-0.04	0.11			
$NB_1, B \rightarrow B$	0.31	0.20	0.43	0.31	0.20	0.43			
$NB_2, B \rightarrow B$	0.81	0.65	0.96	0.81	0.65	0.97			
$NB_3, B \rightarrow B$	1.00	0.20	1.80	1.00	0.20	1.80			

Table 2.7. Comparison statistics for models 1-5 as ranked by QAIC values. QAIC weights are the relative index of each model's likelihood against Model 1.

	Model Description	Deviance	QAIC	Δ QAIC	QAIC weight
Model 1	S(a2) cycle4 P(t)	804.71	554.60	0.00	x
Model 2	S(a2) cycle3 P(t+m)	805.85	555.32	0.73	1.43
Model 3	S(a2) cycle4 P(t+m)	804.71	556.60	2.00	2.82
Model 4	S(a2) cycle5 P(t)	804.71	556.60	2.00	2.72
Model 5	S(a2) cycle5 P(t+m)	804.71	558.60	4.00	7.39

Table 2.8. Relative index of the strength of each model to another based on QAIC weight (row / column).

	Model 1	Model 2	Model 3	Model 4	Model 5
Model 1	x	1.44	2.72	2.72	7.39
Model 2	x	x	1.89	1.89	5.14
Model 3	x	x	x	1.00	2.72
Model 4	x	x	x	x	2.72

Table 2.9. Estimates of reproductive skipping calculated from a frequency distribution from the raw data from the study on Bald Head Island, North Carolina compared to the estimates calculated by Frazer (1983) for Little Cumberland Island, Georgia.

Transition	Current	
	study	Frazer 1983
Breed in 2 consecutive years	0.041	0.036
Skip 1 year	0.322	0.499
Skip 2 years	0.512	0.322
Skip 3 years	0.091	0.112
Skip 4 years	0.033	0.031

Figure 2.1. Map of Bald Head Island, North Carolina. The combined length of all beach represents 15.3km of suitable nesting beach for sea turtles.

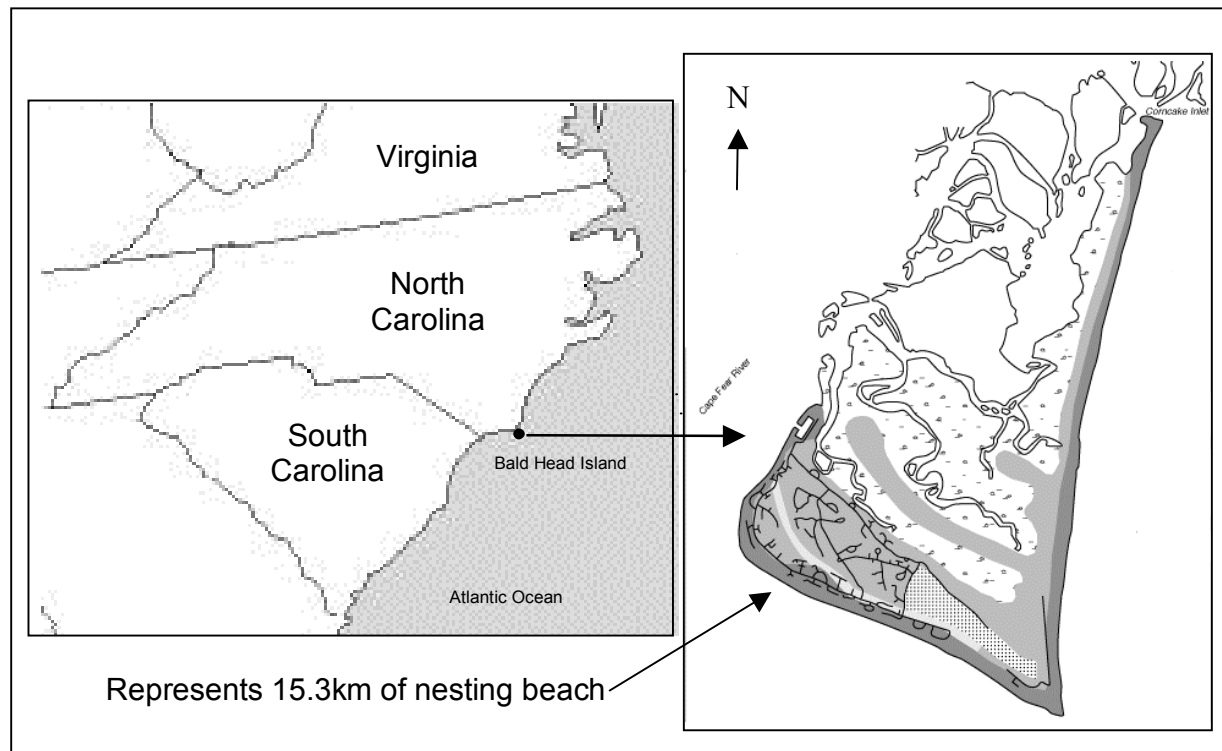


Figure 2.2. Number of loggerhead sea turtle nests laid on Bald Head Island, North Carolina. Points before 1992 may include an insignificant number green sea turtle nests.

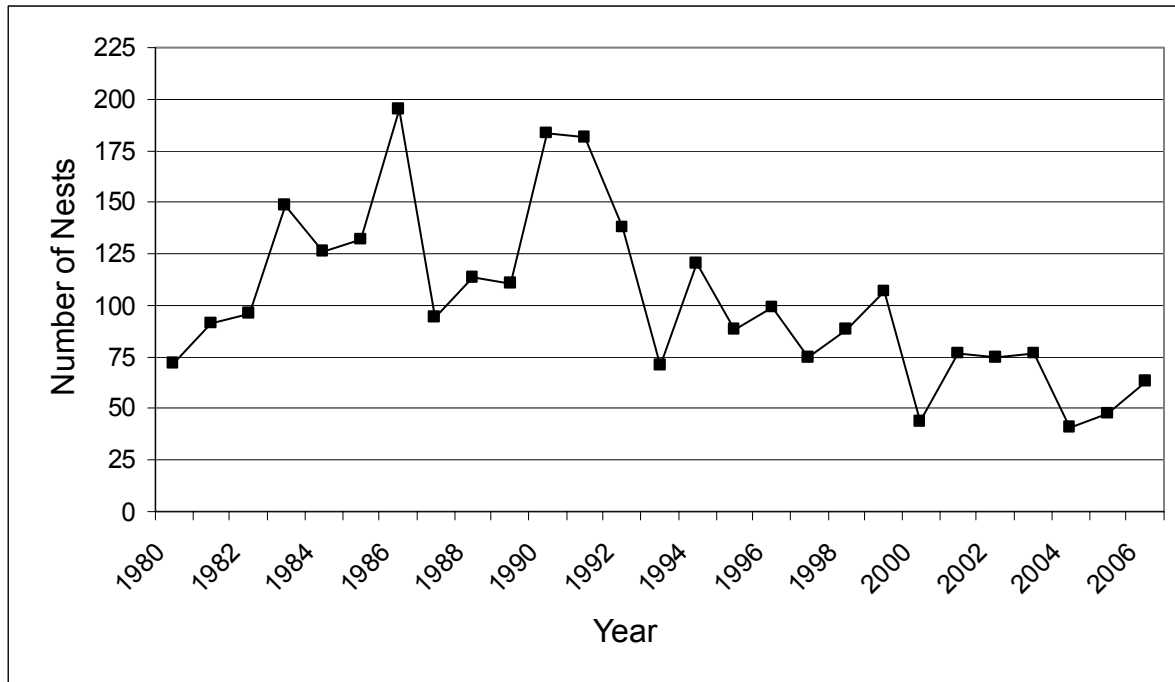


Figure 2.3. Number of years each individual female was observed nesting.

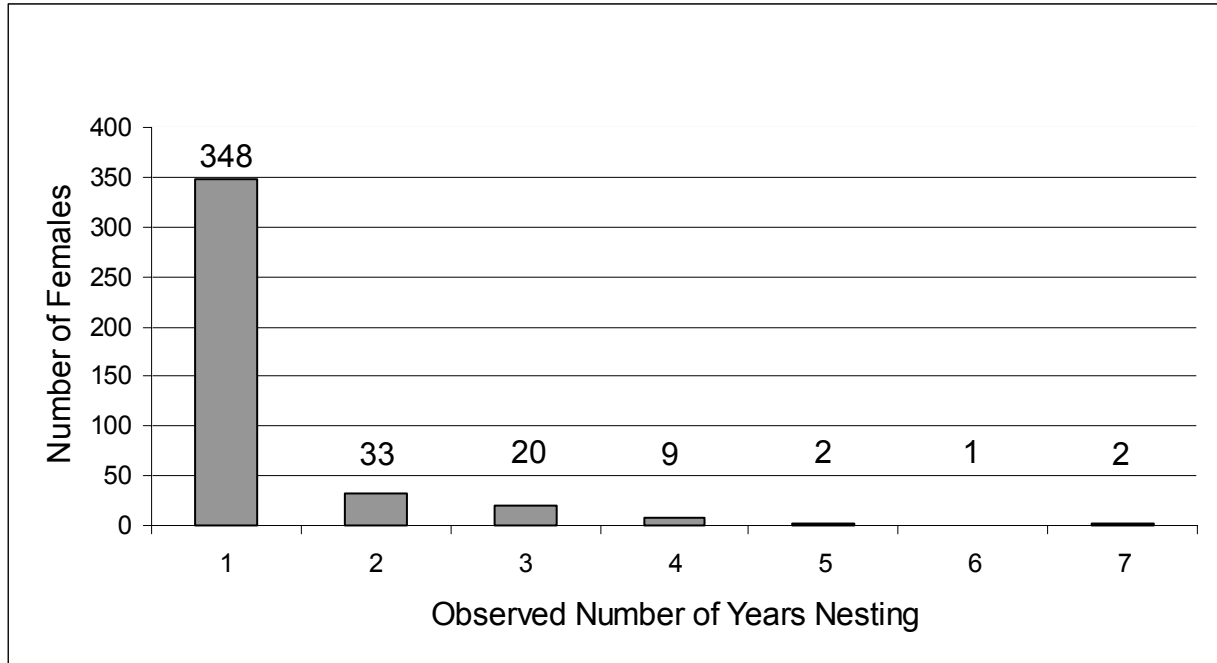


Figure 2.4. Bar graph of minimum number of females nesting per year broken into first capture and remigrants.

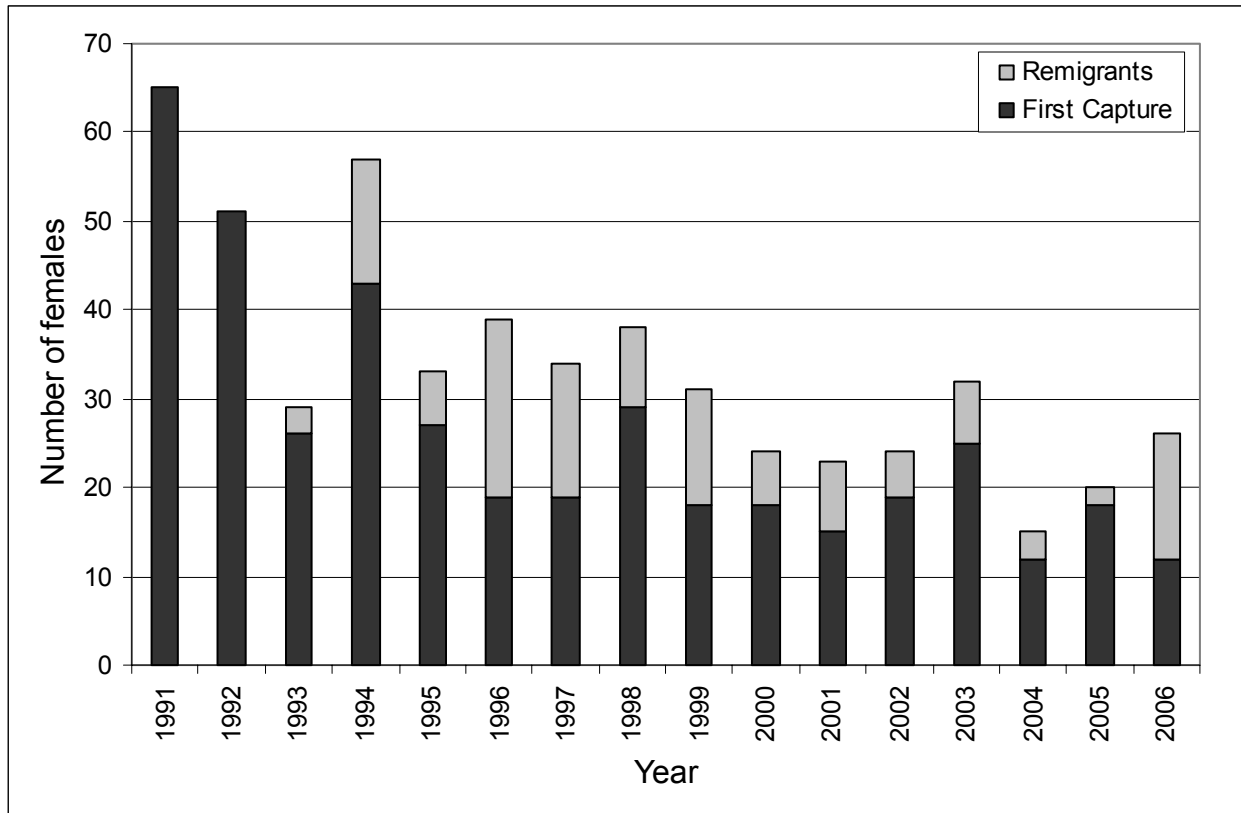


Figure 2.5. Frequency histogram of hatching success rate from 1991-2006 for nests with a hatching success rate greater than 0.0.

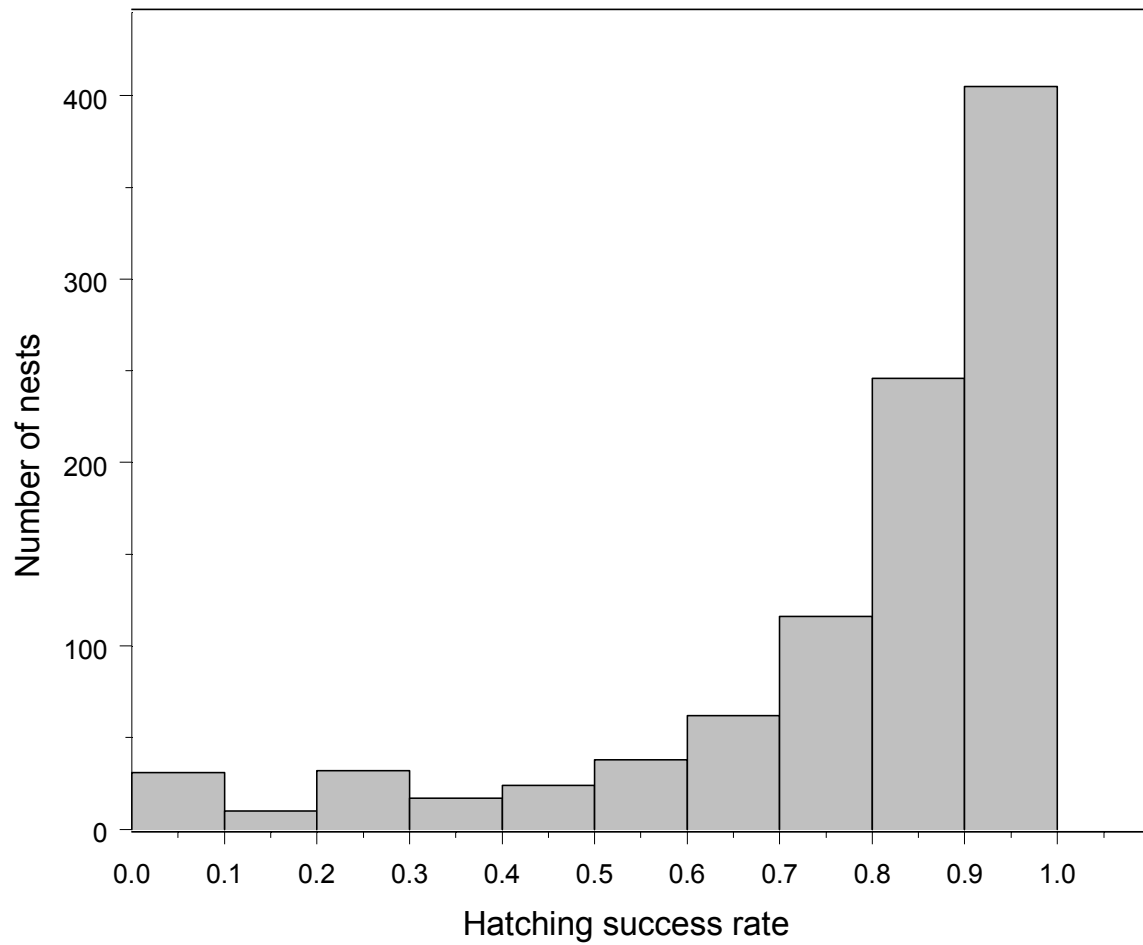


Figure 2.6. Frequency histogram of observed number of clutches laid per season per female for marked females.

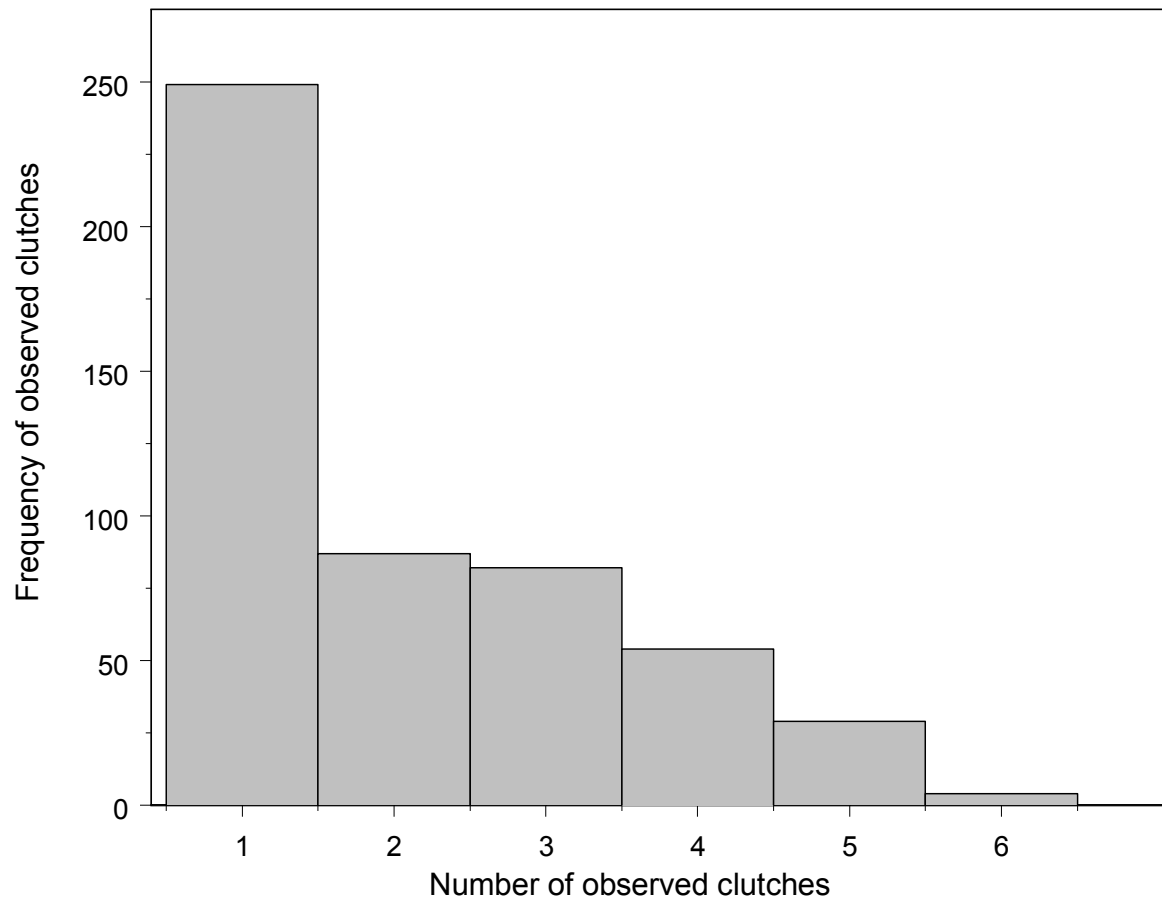
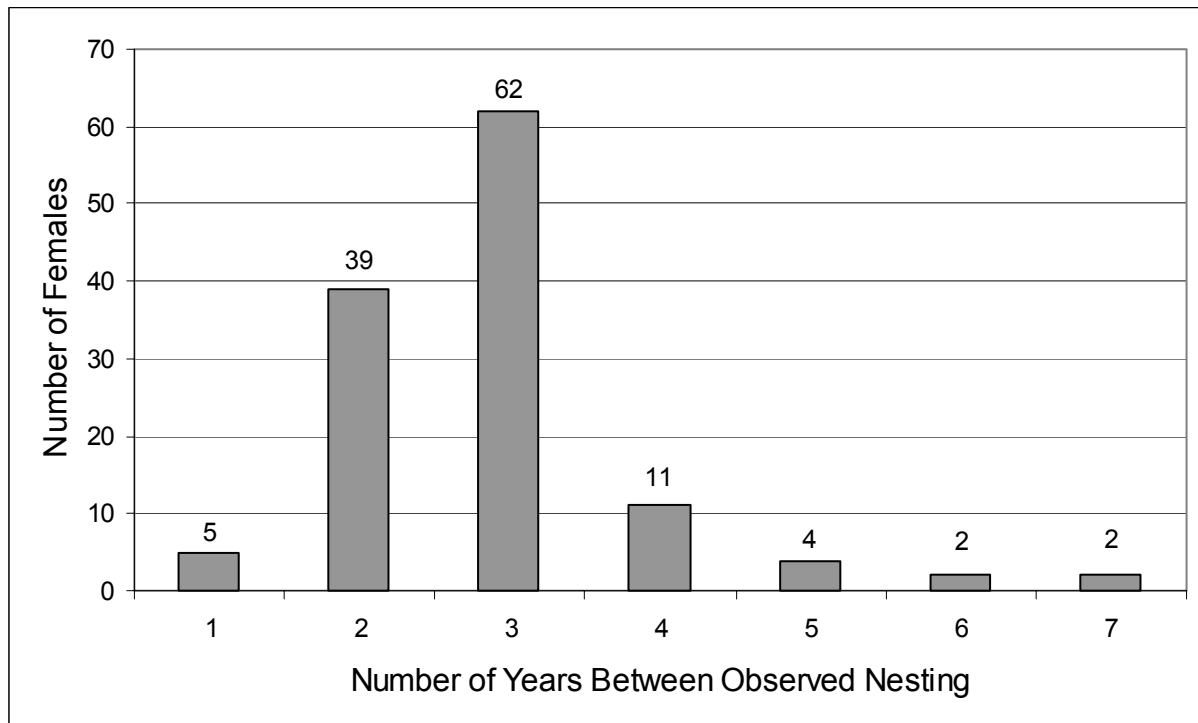


Figure 2.7. Distribution of the number of observed years between nesting for marked females.



CHAPTER 3 – A SIMULATION MODEL FOR LOGGERHEAD SEA TURTLES NESTING IN NORTH CAROLINA, SOUTH CAROLINA, AND GEORGIA, USA

Abstract

Population modeling of loggerhead sea turtles has advanced in the past twenty years as aging techniques and long-term field studies are producing and updating life history parameter estimates. Input parameters for population models are estimates of life history or vital rates that inherently contain various sources of error. Distributions of estimation error are now available for survival rates of benthic juveniles and adults. A population model for loggerheads nesting in North Carolina, South Carolina, and Georgia was created to study the effects of estimation error, clutch frequency, and the larger TED openings on population growth rate and the probability of reaching the nesting recovery threshold defined as 12,800 nests in the three states within the next 50 years. The probability of the population having positive population growth rate was below 50% for all models at all levels of clutch frequency if sub-adult mortality was not decreased. For simulations that included estimation error around benthic juvenile and adult survival rates, but did not reduced mortality on sub-adults estimated up to an 11% probability of reaching the nesting recovery threshold. When sub-adult mortality was reduced and estimation error was included around benthic juvenile and adult survival rates, there was up to a 51% probability of reaching the nesting recovery threshold.

Introduction

An understanding of the population dynamics of loggerhead sea turtles is essential to the successful recovery of the species and its delisting from the Endangered Species Act. However, basic demographic data for the loggerhead sea turtle are limited due to a long generation time and the lack of multiple long-term field studies to estimate life history parameters. For long-lived species such as the loggerhead, matrix models are often employed to explore demographic patterns, determine the effect of varying life stages on population structure, and analyze the population's response to management actions. Matrix models have already played a role in establishing management regulations and determining population recovery probabilities for loggerheads in the United States.

Past loggerhead models did not use survival rates estimated from field-based studies, but fit survival rates to obtain a fixed population growth rate. Most of the parameters input in past models were based on one long-term nesting beach survey on Little Cumberland Island, Georgia (Crowder et al. 1994, TEWG 1998, 2000, Heppell et al. 2003, Frazer 1983). Over the past twenty years field-based studies have greatly increased the knowledge of the loggerhead's life history and provided valuable data for population models. One important discovery was of the genetically distinct subpopulations within the southeastern US nesting aggregation. The subpopulations are only distinct based on mtDNA or maternally inherited DNA, indicating that females return to their subpopulation of birth to nest as adults (Bowen 1993, 1995). Because the matrix population models only account for the female portion of the population and subpopulations are genetically distinct, nesting subpopulations can be modeled independently. One of the recovery goals in the Federal Recovery Plan for loggerhead sea turtles is specific to a

portion of the northern subpopulation (NMFS and USFWS 1991). The recovery goal states: The adult female population in Florida is increasing and in North Carolina, South Carolina, and Georgia, it has returned to pre-listing nesting levels (North Carolina = 800 nests/season; South Carolina = 10,000 nests/season; Georgia = 2,000 nests/season) (NMFS and USFWS 1991). These goals must be sustained for a 25 year period before the population can be considered for de-listing and the subpopulations cannot be de-listed separately.

In this study, the populations were simulated to examine two output criteria: 1) The probability of a portion of the northern subpopulation having a positive growth rate, and 2) the probability of a portion of the northern subpopulation reaching 12,800 nests/season in the next 50 years, hereafter referred to as the nesting recovery threshold. The model only represented females nesting in North Carolina, South Carolina, and Georgia. The goals were met by creating a series of models with the most recent data and incorporating three main effects:

- Incorporation of uncertainty in benthic juvenile and adult survival rates
 - Adult survival rate and breeding transitions from a multistate model (Chapter 2)
 - Benthic juvenile survival rate from Sasso et al. (2006)
- Three levels of clutch frequency
- Decreased sub-adult mortality as a result of new turtle excluder device (TED) regulations

The impacts of the above effects on the population's behavior have not previously been explored and no model has been created specific to one subpopulation. These advances provide both scientists and managers with not only another population model, but actual probabilities of this

population having a positive growth rate and reaching the nesting recovery threshold in the next 50 years.

Uncertainty

Managers often make policy decisions for threatened and endangered species based on the best available data, which are more often sparse for long-lived marine species compared to terrestrial species (Soule 1985, Diamond 1986). Estimates and averages are often used in modeling exercises as point estimates, in which they are assumed to represent the true values of the population (Kendall 1998). However, estimates derived from field studies inherently contain uncertainty, whether it is from measurement error, process error, sampling error, or any other source (Kendall 1998). Simulation modeling is one method used to explore the effect of error on the population's behavior and viability. Clark et al. (1990) stated that sources of uncertainty must be identified and accounted for in management to ensure better management and population recovery. If uncertainty is not included in the analyses used for management recommendations, the worst case scenario could possibly overestimate the probability for the population's persistence (Botsford and Brittnacher 1998).

The uncertainty incorporated in this study was in the form of estimation error around survival rates for benthic juveniles and adults. The survival rates were derived from mark-recapture models and the error (standard deviation) estimated around each mean contains sources of error such as sampling error and measurement error. Data that have been manipulated in any form and originate from a study that was not a complete census of the population have an associated estimation error (Kendall 1998). Estimation error for estimates in this study take the

form of normal density distributions, constructed based on the mean and standard deviation of the estimates.

Benthic Juvenile Survival Rate

A recent mark-recapture study offers new insight into the survival rates for benthic juveniles in the size class (63.6 ± 7.43 cm) (Sasso et al. 2006). An in-water mark-recapture study in Core Sound, North Carolina estimated apparent annual survival rate for benthic juveniles at 0.81 with a standard deviation of 0.06 (Sasso et al. 2006). The survival rate is an apparent survival rate because emigration was not accounted for in the model and will hereafter will be referred to as survival rate (Sasso et al. 2006). This was the first in-water study in North Carolina to estimate an annual survival rate for benthic juveniles and also publish the standard deviation for the estimate. The standard deviation represents the estimation error and allows the survival rate to be incorporated into the model as a distribution, instead of a point estimate as past models have done. Simulations can be run in which benthic juvenile survival rates are randomly drawn from the normal distribution to explore this effect of estimation error on the population's behavior. However, year to year variation cannot be incorporated as there was no time effect on the survival rate estimated.

Adult Survival Rate and Breeding Transition Probabilities

Estimation error around the adult survival rate can be incorporated into the model in the same way as for the benthic juvenile survival rate. An estimate of adult survival rate was estimated in Chapter 2 from a saturation tagging study of nesting females on Bald Head Island, North Carolina. A multistate model was chosen because it models key characteristics of the

loggerhead's breeding patterns. Both reproductive skipping and transience were accounted for in the multistate model structure. Transient individuals are those females that were captured once on the study site, but never in more than one year. The multistate model estimated breeding transition probabilities, annual adult survival rate, and recapture probabilities for females nesting on Bald Head Island. The highest ranked model constrained the breeding cycle to four years, allowing females to spend up to three years as a nonbreeder, before requiring them to breed in the fourth year. The annual survival rate for adult females was estimated at 0.853 with a standard deviation of 0.0365 (Chapter 2).

Clutch Frequency

One factor determining the total observed nests per season is the clutch frequency of breeding females, which ranges from 1-7 in the southeastern United States (Caldwell 1962, Dodd 1988). Even in saturation tagging studies such as on Bald Head Island, not every nesting event is observed and females also have the potential to nest outside the study site. Clutch frequency is individually based within and between seasons making it difficult to extrapolate a "corrected" or estimated clutch frequency from observed clutch frequency (Frazer and Richardson 1985). While observed clutch frequency can be estimated from field work, there is no robust method for converting observed clutch frequency to estimated clutch frequency. A number of methods have been proposed, but none have been empirically tested (Broderick et al. 2002, Rivalan et al. 2006, Addison 1996).

The observed clutch frequency for loggerhead sea turtles nesting on Bald Head Island was estimated at 2.1 nests/season, which represents the minimum estimated clutch frequency (Chapter 2). Only the average estimated clutch frequency is input into population models and

affects the estimated number of nesting females (Schroeder et al. 2003). The average clutch frequency used in population projections by TEWG (1998, 2000) was 4.1 nests/season. This estimated average of 4.1 nests/season was calculated by Murphy and Hopkins (1984) as a “corrected” estimate based on loggerhead sea turtles nesting on Little Cumberland Island, GA. Using different methods, Frazer and Richardson (1985) estimated the range of “corrected” average clutch frequency over a 10-year period as 2.81 - 4.18 nests/season, from observed clutch frequency averages ranging from 2.39 - 3.42 nests/season. The robustness of the methods to calculate the “corrected” or estimated average clutch frequency has not been empirically tested and the distribution of error around estimated clutch frequency is unknown. This study explored the effect of three levels of clutch frequency on probabilities of achieving a positive population growth rate and reaching the nesting recovery threshold in the 50 years modeled. The values of clutch frequency explored included the current range of estimated clutch frequency from the minimum of 2.1 nests/season estimated in Chapter 2 to a maximum estimate in the literature of 4 nests/season. An intermediate estimate of 3 nests/season was also explored.

Turtle Excluder Devices

Population models for loggerhead turtle have often been used to determine the effect of turtle excluder devices (TEDs) on the population (Crowder et al. 1994, Heppell et al. 2003). TEDs have been required in portions of the U.S. shrimp trawl fishery since 1987 (Federal Register 1987). As of December 1994, TEDs were required on all shrimp trawlers year-round (Federal Register 1992a, 1992b) and were expected to reduce the capture of loggerhead turtles by 97% (Henwood et al. 1992). Crowder et al. (1995) analyzed strandings of loggerheads in South Carolina from 1980 - 1993 and noted a 30-40% reduction in overall strandings. However,

it was discovered that the escape opening requirements for TEDs were too small to allow large juveniles to escape (Epperly and Teas 2000). New regulations were implemented in April 2003 requiring a larger escape opening (Federal Register 2002). The effect of the larger TED openings has not yet been applied to a matrix model, but should result in reduced mortality for sub-adult and adult loggerheads.

Model Structure

Matrix models are often employed in population modeling because they possess many valuable properties that allow an understanding of the basic properties of a population, including the population growth rate, the stable age distribution, and the effects of changes in model parameters on the population growth rate (i.e. elasticity analysis) (Caswell 2000). An elasticity analysis examines the effects of proportional changes to matrix elements (survival rates, fertility) on the asymptotic population growth, λ (deKroon 2000). In age-structured models the elasticity analysis helps identify the relative importance of stage class lengths to population growth rates, an uncertainty for loggerhead sea turtle populations.

The most recent loggerhead sea turtle model by Heppell et al. (2003) updated past matrix models with new age-structured data from in-water mark-recapture studies. Heppell et al. (2003) created a hybrid model, with both age-structured and stage-structured components. In age-structured models individuals must advance to the next age-class in the model at each time step whereas in stage-structured models individuals can remain in the same stage class for multiple years (Caswell 2000).

In the model by Heppell et al. (2003), the juvenile stages were age-structured to better detect time lags in the population's response to management, which can be obscured in stage-

based models. The adult stage of the population, including breeders and non-breeders, was stage-structured to include remigration probabilities. The adult stage was also stage-classified because there is no robust estimate for the length of this life stage.

The juvenile stage lengths were elongated based on data from a mark-recapture study in Core and Pamlico Sounds, North Carolina, which estimated the average time required for an individual to grow the 30cm from 50cm to 80cm is 17 years (Braun-McNeill et al. *in review*). The oceanic juvenile stage duration was also lengthened, with new estimates that juvenile loggerheads settle in the benthic environment between 6.5 and 11.5 years of age (Bjorndal et al. 2000). Mark-recapture studies from the Azores estimated annual oceanic juvenile survival rate at 0.911 for ages 2 to 6 (Bjorndal et al. 2003). However, the model in Heppell et al. (2003) used the same survival rate for all ages in the oceanic stage, from oceanic hatchling during year one to age 10. It is realistic that the survival rate for this stage is estimated as lower in Heppell's model because post-hatching migrations to the Azores and juvenile migration to settlement in the neritic zone were included in the survival rate for this stage (Bjorndal et al. 2003).

Methods

Transition Matrix Parameterization

The models in this study represented only nesting females in North Carolina, South Carolina, and Georgia. The mark-recapture study conducted on Bald Head Island, North Carolina only focused on adult females and did not provide any new evidence to the lengths of juvenile age classes. Therefore, stage lengths and size ranges for juvenile stages used in this model originated from “model 2” published by Heppell et al. (2003) (Table 3.1). The projection matrix developed for this study is a hybrid such as that created in Heppell et al. (2003). The

model was a 38x38 matrix based on seven stage classes and represented only the female portion of the population. The seven stage classes included oceanic juvenile, benthic juvenile, sub-adult, breeding adult, non-breeding adult 1 year after breeding, non-breeding adult 2 years after breeding, and non-breeding adult 3 years after breeding (Figure 3.1). The life cycle diagram illustrates all possible transitions for individuals at each time interval. The juvenile life stages are age-structured and the adult life stage, beginning at age 35 is stage-structured. The adult life stage included one breeder state and three non-breeder states. The incorporation of three non-breeder states allowed the breeding transition probabilities calculated in Chapter 2 to be incorporated into the transition matrix. The breeding transitions from Chapter 2 do not represent the same transitions in Frazer (1986) and were incorporated into this model differently than in Heppell et al. (2003).

Survival rates in this model remained the same for oceanic juveniles and sub-adults as published in model 2 from Heppell et al. (2003). The survival rates for benthic juveniles and adults were updated and included in the model as randomly selected estimates from a normal distribution. Benthic juvenile survival rates were drawn from the normal distribution, $N(0.81, 0.06)$ (Figure 3.2) (Sasso et al. 2006). The 95% confidence interval for the benthic juvenile survival rate distribution is fairly wide, with a probability that the randomly drawn survival rate exceeds 1.0. If the survival rate drawn was ≥ 1.0 another estimate was drawn until the estimate was < 1.0 because survival rate of > 1.0 is not biologically possible. This did truncate the distribution, but estimate of ≥ 0.95 were all at the outer tail of the distribution (Figure 3.3). The adult survival rate in Heppell et al. (2003) was replaced with the distribution calculated in Chapter 2, $N(0.853, 0.0365)$. The estimates of benthic juvenile and adult survival rates are annual survival rates and neither of the estimates originated from time dependent survival

models. Therefore, it was assumed that every individual in the population has the same probability of survival every year.

Each column in the matrix from 1 to 34 represented one year in a turtle's life. The population (N) was projected forward as:

$$N_{a+1,t+1} = N_{a,t} * S_a$$

where S is the survival rate for age class a and t is the yearly time step,

$$S_a = 0.875 ; (a = 1, 2, \dots, 10)$$

$$S_a = N(0.81, 0.06) ; (a = 11, 12, \dots, 21)$$

$$S_a = 0.80 ; (a = 22, 23, \dots, 34)$$

The matrix represented a pre-breeding census as females were “counted” before the year's offspring recruit into the population (Caswell 2000). In a pre-breeding birth pulse matrix the survival rate from egg to age one is included in the fertility term (Caswell 2000). The fertility rate (F) was included in element (1,35) of the matrix and was multiplied by the number of breeding females in each year. It was calculated as follows:

$$F = \text{Nests} * \text{Eggs} * \text{Sex Ratio} * S_{\text{egg to hatchling}} * S_{\text{hatchling to age 1}}$$

where the sex ratio represented the average portion of females per nest and S represented the survival rate for the age indicated. The parameters used in this model represent the northern

subpopulation and are as follows: nests = 2.1 (Chapter 2), 3, or 4; eggs per nest = 118 (Chapter 2); sex ratio = 0.58 (Hawkes et al. 2007); survival rate from egg to hatchling = 0.786 (Chapter 2), survival rate to age 1 = 0.875 (Heppell et al. 2003). The estimate of female hatchlings per nest was recently estimated from a sand temperature study on Bald Head Island, North Carolina (Hawkes et al. 2007). Every breeding female was assumed to produce the same number of female offspring that survived to age 1. All of the components of fertility were kept constant for all run except clutch frequency.

The portion of the matrix representing the adults (row 35-38) was constructed as stage-based to include the breeding transition probabilities calculated from the multistate model in Chapter 2. The following represents the adult life stage:

$$\begin{bmatrix} \psi^{B,B} & \psi^{NB_1,B} & \psi^{NB_2,B} & \psi^{NB_3,B} \\ \psi^{B,NB_1} & 0 & 0 & 0 \\ 0 & \psi^{NB_1,NB_2} & 0 & 0 \\ 0 & 0 & \psi^{NB_2,NB_3} & 0 \end{bmatrix}$$

where ψ represents the transition probability. The superscript describes the transition being made by each individual, where B represents the breeder state, and NB represents the non-breeder state. The subscript on the non-breeder states represents the number of years spent as a non-breeder. The transition probabilities are the probabilities of moving between the breeder and non-breeder states. For example, transition B,B represents the probability of an individual breeding two years in a row whereas transition B, NB_1 is the probability of becoming a non-breeder in year $t+1$ after breeding in year t . Individuals must always advance to the next non-breeder state in each time step unless returning to breed. The probability of breeding two years

in a row is 0.03, of skipping one year before returning to breed is 0.31, skipping two years before returning to breed is 0.81, and skipping three years before returning to breed is 1.0 (Chapter 2).

Model structures

Six models were created to investigate the effects of including estimations error around survival rates and the increase in sub-adult survival rate expected from the introduction of larger TED openings. Three variants of each model were run, incorporating the three alternate values for clutch frequency.

The first four models focused on the effect of estimation error in survival rates on having a positive growth rate and the probability of the northern subpopulation from North Carolina, South Carolina, and Georgia reaching the nesting recovery threshold. The survival rates were either “constant” for all runs in a simulation or drawn from a distribution for each run. The survival rates for oceanic juveniles and sub-adults were always constant. When the survival rates for benthic juveniles and adult were constant, the survival rates used were 0.81 and 0.853, respectively. The first four models were structured as follows (Table 3.2):

Model 1: All survival rates constant

Model 2: Benthic juvenile survival from distributions, all other survival rates constant

Model 3: Adult survival rate from distributions, all other survival rates constant

Model 4: Adult and benthic juvenile survival rates from distributions, all other survival rates constant.

Models 5 and 6 explored the effect of larger TED openings on the sub-adult stage. To examine the effect of the new regulation two models were created that included a 30% reduction of mortality on sub-adults (Crowder et al. 1995, Heppell et al. 2003), hereafter referred to as the TED effect. Crowder et al. (1995) observed a 30% decrease in strandings on beaches in South Carolina after the 1994 implementation of TEDs. The decrease in mortality is estimated for sub-adults following the larger TED openings required as of 2003 should be seen now that all large sub-adults can escape (Epperly and Teas 2000).

The resulting reduction in mortality increases sub-adult survival rate to an estimate of 0.86. Mortality was not reduced on the benthic juvenile stage in this study. The study by Epperly and Teas (2000) predicted the minimum straight carapace length for turtles with a body depth too large to fit through the pre-2003 TEDs to be 79.8cm. For this model, that only represents the sub-adult and adult life stages. The models including the TED effect were parameterized as follows:

Model 5: All survival rates constant

Model 6: Benthic juvenile and adult survival rates from distributions all other survival rates constant

Each of the 6 models was run with the average clutch frequency per female or nests/season at 2.1, 3.0, and 4.0. The estimate of 2.1 is the average observed nests/season for females nesting on Bald Head Island, North Carolina (Chapter 2). However, observed clutch frequency is biased low due to a capture probability of less than 1.0 and imprecise nesting site fidelity (Broderick et al. 2003). The estimates of higher clutch frequency were modeled to

compare population growth rates and probability of reaching the nesting recovery threshold in each model.

The model was projected for 50 years and each time step in the model represented one year. From 1989-1998 the total number of nests ranged from 3,592 to 6,532 which average about 5000 nests/season (TEWG 2000). The initial populations were calculated based upon the stable age distribution and so that every run began with 5000 nests laid in year one. The stable age distribution of each run in a simulation was calculated from the matrix after the estimates of benthic juvenile and adult survival rates were drawn from their distributions. To convert the stable age distribution to an initial population, the number of breeders needed to lay 5000 nests was calculated for each level of clutch frequency. This resulted in 2831 breeders at a clutch frequency of 2.1 nests/season, 1667 breeders at 3 nests/season, and 1250 breeders at 4 nests/season. Each initial population had a different total population size.

In models 2, 3, 4 and 6, in which estimates of benthic juvenile and/or adult survival rates were drawn randomly from the distribution the same survival rate was used for all 50 years of the projection. This is because the error was due to estimation error around the value of the parameter, not an estimate of year-to-year variation. A new estimate was drawn in year one for each of the 1000 runs of a simulation. Therefore, since there was no year-to-year variation, each of 1000 runs of a simulation had a constant population growth rate. The population growth rate was tracked for each run to determine the proportion of runs in a simulation that produced a positive growth rate over the 50 years modeled. Neither density dependence nor population extinction probabilities were included in this study because only a portion of one subpopulation was modeled in this study. Density dependence could be included if a maximum number of nests per suitable beach mile were available.

The nesting recovery threshold was based on the number of nests/season as indicated by the Federal Recovery Plan for loggerhead sea turtles (NMFS & USFWS 1991). The recovery and delisting goal for this portion of the northern subpopulation is 12,800 nests laid per year in the three states for 25 consecutive years. This study looked at the probability of reaching 12,800 nests/season, the nesting recovery threshold, by the end of the 50 year time period modeled.

Elasticity Analysis

Elasticity analyses were conducted for models 1 and 5 where constant survival rates are used for all stage classes. Elasticities ($E_{i,j}$) from matrix (A) were calculated from the stable age distribution and reproductive value of A :

$$E_{i,j} = \frac{\partial \lambda}{\partial A_{i,j}} \frac{\lambda}{A_{i,j}} = \frac{v_i \omega_j}{\langle v, w \rangle}$$

where $\langle v, w \rangle$ is the scalar product of the two eigenvectors (Caswell 2000). The elasticity analysis from this model is only directly comparable to that from Heppell et al (2003) because it is the only other published hybrid model with similar stage lengths for loggerhead sea turtles. The elasticities of population growth rate to changes in each age in a stage class were summed to obtain the elasticity for each stage. The elasticities of population growth rate to changes in the three non-breeder states were also summed. All of the elasticity analyses and simulations were implemented using MATLAB (2005).

Results

Model 1, which projected the population using the constant survival rates, produced negative growth rates for all three values of clutch frequency (Table 3.3). When the clutch

frequency was set to 2.1 nests/season the model estimated that after 50 years there would be less than 1800 nests per year in North Carolina, South Carolina, and Georgia combined. Even with every breeder laying 4 nests/season there would only be 3939 nests laid in year 50, 30% of the nesting recovery threshold (Figure 3.4). The population declined at a much slower rate of -0.5% per year when the value of nests per season was set to 4, as compared to -1.2% per year at 3 nests/season and -2.0% per year at 2.1 nests/season. The trajectories of nests/season and breeders per year depict the effect clutch frequency has on population growth rate (Figure 3.5).

Models 2-4 introduced the estimation error associated with drawing benthic juvenile and adult survival rates from distributions. Each of these distributions originated from field studies. Because the error distribution around the estimate of the benthic juvenile survival rates includes values as high as 0.98, when high values such as these were randomly drawn in the simulations the projections produced a population explosion (Figure 3.6). In reality, density dependence would come into play, but was not modeled here. While no runs ever reached zero breeders in any year, runs with only 13 breeders in year 50 could be possible. However, no extinction threshold was created because the model only represented a portion of the northern subpopulation.

The distribution of population growth rates for model 2 are found in Figure (3.7), with the median increasing as clutch frequency increases. At 3 nests/season many of the outliers fall on the lower side of the distribution indicating the population in some model runs was decreasing at greater than -6% annually. In model 2 with nests/season set at 2.1 only 11% of the run resulted in a positive growth rate, compared to 25% at 3 nests/season and 42% at 4 nests/season. The probability of reaching the nesting recovery threshold followed the same pattern and under

the best circumstance, when the value of nests/season was set to 4, there was only a 10% probability of reaching 12,800 nests by year 50.

Model 3, in which only the adult survival rate was drawn from a distribution, resulted in a right-skewed distribution for population growth rates (Figure 3.8). It also produced the tightest distribution, of output of all the models which incorporated error, due to the small standard deviation associated with the adult survival rate. When the value of nests/season was set at 2.1, less than 1% of the runs resulted in a positive growth rate. At 3 nests/season, only 5.5% of the runs produced a positive growth rate and at 4 nests/season, only 21% of the runs resulted in a positive growth rate. Only one run at 3 nests/season and two runs at 4 nests/season reached the nesting recovery threshold by year 50. To reach the nesting recovery threshold in year 50 for model 3 adult survival rate had to reach a value greater than 0.976 at 3 nests/season and greater than 0.96 at 4 nests/season. The reduced probability of a positive growth rate in model 3 in comparison to model 2 was expected based on the results of the elasticity analysis, which shows that a proportional change in benthic juvenile survival rate has a larger effect on the population growth rate than a proportional change in adult survival rate (Figure 3.9).

Model 4, where both benthic juvenile and adult survival rates were drawn from distributions, produced a population growth rate distribution that was much wider than those for models 2 and 3 (Figure 3.10). The median population growth rates associated with the three values of clutch frequency were between 0.98 and 1.0. The probability of achieving a positive growth rate with the value of nests/season at 2.1 was 15%. If the clutch frequency was increased to 3 nests/season the probability rose to 25% and, similarly, when the clutch frequency was increased to 4 nests/season, the probability rose to 41%. The nesting recovery threshold was

reached in only 1% of runs when females laid 2.1 nests/season, 5% of runs at 3 nests/season, and 11% of runs at 4 nests/season.

Models 5 and 6 both included the TED effect on sub-adult survival rate, increasing the annual survival rate to 0.86 from 0.8. Model 5, the deterministic model, produced positive growth rates for the population for all three values of nests/season (Figure 3.11). Only when the value of nests/season was set at 4 did the population reach the nesting recovery threshold with the 50 year time period (Table 3.5, Figure 3.12).

Model 6, which included the TED effect and estimation error distributions around both benthic juvenile and adult survival rates produced a higher median population growth rate and a more left-skewed distribution as clutch frequency increased (Figure 3.13). While all of the median growth rates were above 1.0, outliers in the distribution resulted were able to produce a population which declined by as much as -8% per year. When the value of nests/season was set to 2.1, a positive rate was produced in 57% of all runs. For nests/season set at 3, 73% of all runs produced a positive growth rate and for 4 nests/season, 83% of all runs resulted in a positive growth rate. Only 18% of the runs reached the nesting recovery threshold when nests/season was set at 2.1. At 3 nests/season there was a 37% probability of reaching the nesting recovery threshold and a 51% probability at 4 nests/season. The probabilities of a population with a positive growth rate are highest in model 6 at all levels of clutch frequency. Model 6 is also the only model that had any simulation with a >50% probability of reaching 12,800 nests/year in 50 years.

There were minimal differences in the elasticities between models with different values for nests/season. There are also minimally detectable differences in the models with and without the TED effect (model 1 vs. model 5) (Figure 3.9). Changes in the sub-adult survival rates have

the largest proportional impact on the population growth rate whereas fertility has the smallest. It is important to note that the fertility term included the survival rate to age one. The survival rate of non-breeders had a higher elasticity than breeders simply because a larger portion of the adult population is in the non-breeder state in any one year.

Discussion

This study was the first to model loggerhead sea turtles nesting in only North Carolina, South Carolina, and Georgia and was the first for loggerheads include uncertainty around parameter estimates. The majority of model parameters originated from studies either on nesting beaches or in the waters of North Carolina. Studies have shown that juveniles in the northern portion of the range grow at a slower rate than juveniles residing in the waters of the Bahamas and Florida, which ultimately affects the stage lengths and age at sexual maturity (Bjorndal and Bolten 1988, Mendonca 1981). Therefore, it is important to stress that the models are specific to the northern subpopulation.

Uncertainty

Past modeling exercises for loggerhead sea turtles have acknowledged uncertainty in parameter estimates and model output, but did not have the distributions of estimation available in this study. The output from this study included a portion of the uncertainty in the system and provides managers with probability distributions of the population growth rate and distributions of reaching the nesting recovery threshold. The model output distributions are more informative than point estimates and will allow for more informed management decisions to be made (Parysow and Tazik 2001). While the results only indicated the probability of reaching the

nesting recovery threshold, all of the model runs which produced a positive growth rate would eventually reach 12,800 nests.

Estimation error around benthic juvenile and adult survival rates proved to play an important role in the population growth rate and probability of reaching the nesting recovery threshold. Past models estimated juvenile survival rates by fitting them to a fixed population growth rate and were not based on field studies for each life stage (Crowder et al. 1994, Heppell et al. 2003). The incorporation of uncertainty in the form of estimation error is becoming more common as the data from long term studies become available. Uncertainty has been included in population models for threatened and endangered species such as the North Pacific humpback whale (Gerber and DeMaster 1999) and the black-capped vireo (Parysow and Tazik 2002). Uncertainty was incorporated in these analyses to determine similar effects as in this study, the probability of a positive population growth rate and reaching certain recovery criteria. Including uncertainty in these analyses provided managers with more informed data than a single point estimate from parameter averages, and therefore more appropriate management for the species (Boyce 2000, White 2000). The only sea turtle model incorporating uncertainty was created for a green sea turtle population in the southern Great Barrier Reef (Chaloupka 2002). The model included sampling error, measurement error, environmental stochasticity, and year-to-year demographic variability to determine the population's ability to sustain a harvest.

The incorporation of uncertainty in this study shed light on the importance of estimation error to predicting the probabilities of reaching management goals. Incorporating estimation error into only one of the survival rates as in models 2 and 3, illustrated the changes each rate independently has on the population growth rate. When estimation error around both benthic juvenile and adult survival rates was included in the model, the resulting distribution of

population growth rates included more error than if just one of the survival rates was drawn from a distribution. A wider output distribution is expected as more error is included in model input. The distribution of population growth rate for model 4 contained outliers from runs in which the combination of benthic juvenile and adults survival rates were both drawn from the outer tails of their associated distributions. For runs in which both of the survival rates were drawn from the right tail of the distribution, the population exploded and if both estimates were drawn from the left tails of the distributions the population crashed.

The distributions of population growth rates for models with estimation error provided a more conservative outlook on the population's status than the point estimates from models 1 and 5. Looking at the population growth rates from model 5, one might assume that the population will have a positive growth rate at all levels of clutch frequency. However, the distributions of population growth rates produced from model 6 indicate a probability that the population growth rate may be negative at any level of clutch frequency (Figure 3.13).

Multistate Model

The distribution of adult survival rates used in this model is the first for loggerhead sea turtles estimated from a multistate model. A multistate model is a more appropriate method to determine survival and breeding transition probabilities than methods used in the past. Adult survival rates were previously estimated using Cormack-Jolly-Seber (CJS) models (NMFS 2001). However, a CJS model violates assumptions for sea turtle mark-recapture data collected on a nesting beach. The CJS model does not account for reproductive skipping or the presence of transient individuals in the population, whereas the multistate model can account for both.

The only estimate for breeding transition probabilities other than from the multistate model in Chapter 2 are from Frazer (1983). Frazer (1983) calculated the remigration intervals and survival probabilities independently. However, this biases the estimates of both survival and remigration intervals because the two are correlated. The multistate model accounted for this correlation, reducing bias on the estimates.

The only limitation of the estimate of adult survival rate and the benthic juvenile survival rate is that neither was estimated from survival models with a time effect. Therefore, while it is not biologically realistic that annual survival for these life stages would be constant over a 50 year time period, year-to-year variation could not be incorporated into the model without violating assumptions.

Clutch Frequency

The simulations demonstrated that average clutch frequency input in a model can have a dramatic effect on the population growth rate and probability of reaching the nesting recovery threshold. In recent loggerhead projection models, the estimate of 4.1 nests/season (Murphy and Hopkins 1984) was input into projection models as the average clutch frequency (TEWG 1998, 2000, Heppell et al. 2003). However, the estimate was never published in the peer-reviewed literature and the methods used to calculate the estimate were never validated with field data.

There is a general consensus that females lay 1-7 nests/season and for the average to be 4 or higher, the distribution of clutch frequency would have to be skewed toward the higher end of the range. This is not out of the realm of possibilities, but should be considered a high estimate given the limited knowledge of the actual distribution and observed average clutch frequencies from Little Cumberland Island, GA (Frazer and Richardson 1985).

As the simulations in this study demonstrate, an average clutch frequency of 2.1, 3 or 4 nests/season produced very different population probabilities for a population growth rate and even larger differences in population size. To be conservative, the results from models using clutch frequency set at 4.1 nests/season should be interpreted as representing a maximum average clutch frequency. Based on the published estimates of observed clutch frequency, the results from models with clutch frequency set at 3 nests/season should be considered more likely. More research is needed to produce a robust estimate or distribution for clutch frequency. This is especially important if clutch frequency is only input into the model as an average point estimate.

Turtle Excluder Device Effect

The TED effect had the expected positive impact both population growth rate the probability of reaching the nesting recovery threshold. The two most recognized models that have previously examined the effect of TEDs on loggerhead populations were Crowder et al. (1994) and Heppell et al. (2003).

From a stage-based model, Crowder et al. (1994) found that proportional changes in the large juvenile stage survival rate resulted in the largest proportional changes of population growth rate. While the elasticity analysis in Crowder et al. (1994) exhibited a different pattern than from this model, the juvenile stages were identified as the most “important” in both models. Crowder et al. (1994) also determined that a 20% decrease in large, juvenile, sub-adult, and adult mortality could result in the recovery of loggerhead populations in the southeastern US.

Heppell et al. (2003) ran simulations with a 30% reduction in mortality on varying stage classes. The model did not produce a positive population growth rate when mortality was reduced for only the small neritic (benthic juvenile in this study) life stage. However, reduced

mortality on both small and large neritic (benthic juvenile and sub-adult in this study) life stages or both neritic and adult life stages resulted in a positive population growth rate of less than 2% per year.

The median annual population growth rate for model 6 was positively increasing by 2% per year at 4 nests/season (Figure 3.13). If 4 nests/season represents a high average clutch frequency, the median probability of an increasing population at 2% annually also represents a maximum average. The distributions of population growth rates for model 6 at 2.1 and 3 nests/season are more conservative. However, overestimating the probability of a population growth rate for a threatened species is not precautionary and would result in inappropriate management policies.

While the model structures in this study differed from those in Crowder et al. (1994) and Heppell et al. (2003), all indicated that the requirement of TEDs is a step in the right direction to recovering the population of loggerhead turtles. However, the implementation of a policy that requires larger TEDs alone is unlikely to create a population growth rate high enough to result in reaching the nesting recovery threshold or recovery goal in the next 50 years. Other sources of mortality must be identified and reduced to ensure higher probabilities of success towards rebuilding the population.

Elasticity analysis

The elasticity analysis for a model is often used to identify parameters or life stages that are most “important” to manage when the goal is to increase the population growth rate (Heppell et al. 2000). Many of the results from this study were expected from studying the elasticity

analysis, but there are two components of the models in this study that deserve comment in regard to the elasticity analysis, fertility and the stage-structured adult life stage.

The difference in results of the simulations from models 2 and 3 were expected based on the results of the elasticity analysis (Figure 3.9). Model 2 produced a larger proportion of simulations with a positive growth rate at all levels of clutch frequency than those from model 3. Benthic juvenile survival rate in model 2 must increase by 5% from the mean estimate of 0.81 and adult survival rate in model 3 must increase by 7% from a mean of 0.853 for the model to produce a population with a positive growth rate. The sub-adult survival rate was increased by 7.5% and used consistently in every run of model 6. Therefore, the higher probabilities of reaching a positive growth rate in model 6 are explained by the elasticity analysis as a proportional change in the sub-adult survival rate results in the largest change in population growth rate.

One of the effects explored in this study that could potentially affect management, but was not revealed by the elasticity is the effect of clutch frequency on the population projections. A proportional change in fertility had the smallest impact on changes in population growth rate, which may be misleading to managers. Increasing the clutch frequency in the model from 2.1 nests/season to 3 nests/season results in a 42% increase in the fertility term, which is a large proportional increase. While it does not have the same impact on the population growth rate as a 42% increase in sub-adult survival, the models have shown that clutch frequency values of 2.1, 3, or 4 nests/season provided different probabilities of a positive population growth rate and reaching the nesting recovery threshold. Doubling the clutch frequency ultimately doubled the population size over time. This illustrates the need to look beyond the elasticity analysis when determine management strategies.

For the stage-structured adult stage, the length of that stage is not a factor in the elasticity analysis. In an age-structured model the proportional changes to population growth rate for stage class survival rates are dependent on the number of age classes in each stage (Caswell 2000).

Modeling Subpopulations

It is important to create models for individual nesting subpopulations since studies have indicated that that growth rates and age at sexual maturity may differ between subpopulations (Bjorndal and Bolten 1988, Mendonca 1981). This has an impact on model structure and population's response to management actions. Modeling the subpopulations independently produces a more informative description of the overall population than using parameter values averaged across all subpopulations

Appropriate Time Durations to Model

Beissinger and Westphal (1998) suggested modeling shorter time frames for population projections to explore short term management needs rather than long term population viability. The population in this study was modeled with a constant population growth rate over the 50 year period because distributions representing the effects of demographic and environmental stochasticity are not known for loggerhead sea turtles. The results in this study as well as those in Crowder et al. (1994) and Heppell et al. (2003) indicated that the probability of 12,800 nests, whether once as in the nesting recovery threshold, or for 25 consecutive years as in the recovery criteria, could easily be more than 50 years into the future.

One characteristic of population models is that with each time step of the model projection, error is compounded (Beissinger and Westphal 1998). Model results become less

applicable as the population is projected further into the future, particularly when the distribution of error around all parameter estimates is unknown (Beissinger and Westphal 1998). In addition, management actions and environmental conditions are likely to change over time in unpredictable ways, making shorter term projections likely to be more useful than the more length projections associated with traditional population viability analyses. Therefore, there is more confidence in the probability distribution of model output in year 50 of a projection than in year 100.

Adding Mileposts to Recovery Goals

Results from this study and previous studies have demonstrated the lengthy process that will likely be required to recovery the loggerhead sea turtle population. The requirement for the northern subpopulation not only to reach 12,800 nests, but then maintain that number for 25 consecutive years is a long term challenge. Because of this and because of the difficulties in modeling a population at a great number of years into the future for the reasons described above, it would be useful to create one or more mileposts in addition to the ultimate recovery criteria. The nesting recovery threshold, defined as reaching 12,800 nests within 50 years may be one possible milepost to consider. This study projected the population 50 years into the future, but other timelines could also be considered.

In addition to allowing for more applicable population projection models, mileposts would allow managers and stakeholders to get a better sense as to how much progress is being made towards population recovery. Reaching a milepost would be less daunting and provide an earlier success than the ultimate effort and time required for full recovery. A milepost such as

the nesting recovery threshold would definitely not replace the recovery goal as in the Federal Recovery Plan, but would suggest focusing on shorter term goals as well.

Management Implications

From the range of model simulations, and assuming the model structure best represents the northern subpopulation, recommendations can be made for management. The requirement for enlarged openings in TEDs to increase sub-adult survival provides clear benefits. While the elasticity analysis suggests increasing the survival rates of juvenile stages have the largest proportional impacts on the population growth rate, the importance of managing all life stages should not be dismissed.

A recent management action of requiring circle hooks in the longline fishery in the northwestern Atlantic will reduce mortality on juvenile and adult life stages (Federal Register 2004). Large scale management actions such as this are needed to reduce mortality on the juvenile survival rates.

While actions have been taken in the trawl and longline fisheries, there are still other fisheries whose management would benefit sea turtles. Two of these fisheries that affect turtles in North Carolina waters are gill net and pound net fisheries. Both fisheries affect the juvenile and adult life stages. Any decrease in the mortality rate of juvenile stage classes especially, will increase the probability of a positive growth rate for the population.

Fertility does not have the highest proportional impacts on population growth rate, but management actions should still be taken on nesting beaches. If adult females are forced to nest in suboptimal locations or hatchlings are not recruited into the population, there is that much of a smaller probability that the population growth rate will increase.

Future Research

The models in this study have revealed that estimation error has an effect on the probability of producing a positive population growth rate and reaching the nesting recovery threshold. While the elasticity analysis revealed that a proportional change in the sub-adult survival rate results in the greatest population growth rate change, the modeling exercise indicated the elasticity analysis should not be the only factor used to identify areas of further study or management. From this study future directions for field studies and modeling can be suggested.

Field studies should now focus on understanding the uncertainty in sub-adult survival. This can be accomplished through an in-water survey such as that conducted in Sasso et al. (2006) for benthic juveniles. Because proportional changes in sub-adult survival have the greatest impact on the population growth rate, determining an estimate with an associated error distribution should be a key priority.

Another need identified by this study is an understanding of the distribution of estimated clutch frequency. As seen in the results of this study, clutch frequency directly affects reproductive output and population size. There are few long term mark-recapture studies conducted along the southeastern coast of the United States that can estimate observed clutch frequency. A more informative, but conservative solution would be to include estimates of the distribution for observed clutch frequency into the model, if available. The resulting distributions would be more informative than inputting one average or several alternative values of clutch frequency into the model. The most realistic, but expensive solution to estimating clutch frequency would be to deploy a sufficient number of satellite transmitters at the start of a nesting season (Hays et al. 1991, Hays 1992).

The data from Sasso et al. (2006) was also recently fitted to a different model that resulted in a smaller standard deviation (C. Sasso pers. comm.). The new distribution for benthic juvenile survival should be incorporated into this model when it becomes available. The smaller confidence error around the new estimation will increase the confidence in model output probabilities.

In Conclusion

Ultimately, a tremendous amount of uncertainty exists in our understanding of the population dynamics of loggerhead sea turtles. This impacts our ability to model the current and future status of the population. Improved estimates of life history parameters and improved model structures are necessary to reduce the uncertainty, better understand the species, and ultimately aid managers in making important policy decisions. This study has made progress in both, incorporating estimation error into the model and applying a multistate model structure for both adult survival estimation and population projections.

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Table 3.1. Stage lengths and survival rates used in the matrix model. The standard deviation of the estimate is in parentheses where available. Size range and stage length are from “model 2” in Heppell et al. (2003).

	Oceanic juvenile	Benthic juvenile	Sub-adult	Adult (breeder & non-breeder)
Size range	4-45cm	45-72cm	72-92cm	>92cm
Stage Length	10	11	13	35+
Survival estimates	.875	.81 (.06)	.81 .86 (TED effect)	.853 (.0365)
Source of survival estimate	Heppell et al. 2003	Sasso et al. 2006	Heppell et al. 2003	Chapter 2

Table 3.2. Description of survival rates input into models 1-6. The “C” denotes a constant survival rate used for all 1000 model runs, “D” denotes the survival rate was drawn from a distribution at year one of ever 1000 runs. TED effect indicates a 30% reduction in mortality for the sub-adult stage.

	Oceanic juvenile	Benthic juvenile	Sub-adult	Adult (breeder & non-breeder)
Model 1	C	C	C	C
Model 2	C	D	C	C
Model 3	C	C	C	D
Model 4	C	D	C	D
Model 5	C	C	C TED effect	C
Model 6	C	D	C TED effect	D

Table 3.3. Results from model 1 for each level of nests/season. Breeders and nests are from year 50 of the projection and λ is the population growth rate.

	Nests / season	λ	Breeders	Nests
Model 1: constant survivals	2.1	0.980	847	1778
	3	0.988	919	2757
	4	0.995	985	3939

Table 3.4. Simulation results for models 2-4 for each level of nests/season. The results are the number of runs, out of 1000, in which the annual population growth rate, λ , was ≥ 1.0 and the nests/season recovery goal of $\geq 12,800$ nests was met in year 50 of the projection.

	Nests / season	$\lambda \geq 1.0$	Nests/year $\geq 12,800$
Model 2: benthic juvenile survival from distribution	2.1 3 4	114 256 427	5 41 102
Model 3: adult survival from distribution	2.1 3 4	8 55 213	0 1 2
Model 4: benthic juvenile & adult survival from distributions	2.1 3 4	153 256 411	10 54 114

Table 3.5. Results from model 5 for each level of nests/season. Breeders and nests are from year 50 of the projection and λ is the population growth rate.

	Nests / season	λ	Breeders	Nests
Model 5: TED effect, constant survivals	2.1	1.003	2716	5703
	3	1.001	2980	8939
	4	1.019	3219	12874

Table 3.6. Simulation results for model 6 for each level of nests/season. The results are the number of runs, out of 1000, in which the population growth rate, λ , was ≥ 1.0 and the nests/season recovery goal of $\geq 12,800$ nests was met in year 50 of the projection.

	Nests / season	$\lambda \geq 1.0$	Nests/year $\geq 12,800$
Model 6: TED effect, benthic juvenile & adult survival from distributions	2.1	570	187
	3	728	377
	4	827	510

Figure 3.1. Life cycle graph for loggerhead matrix model. Each node represents one year and females can spend up to 3 years as a non-breeder.

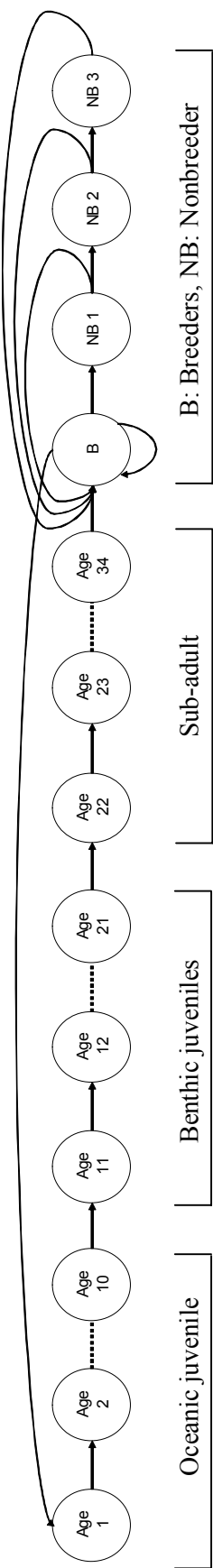


Figure 3.2. Frequency histogram of 1000 randomly selected annual benthic juvenile survival rates from $N(0.81, 0.06)$. The distribution was truncated at 1.0.

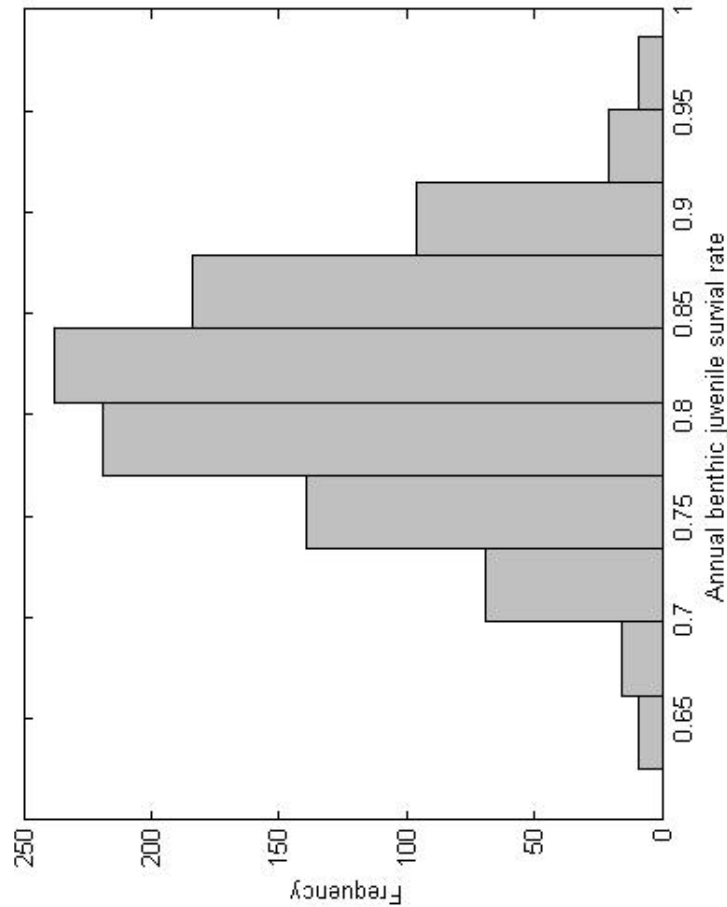


Figure 3.3. Frequency histogram of 1000 randomly selected annually adult survival rates from $N(0.853, 0.0365)$.

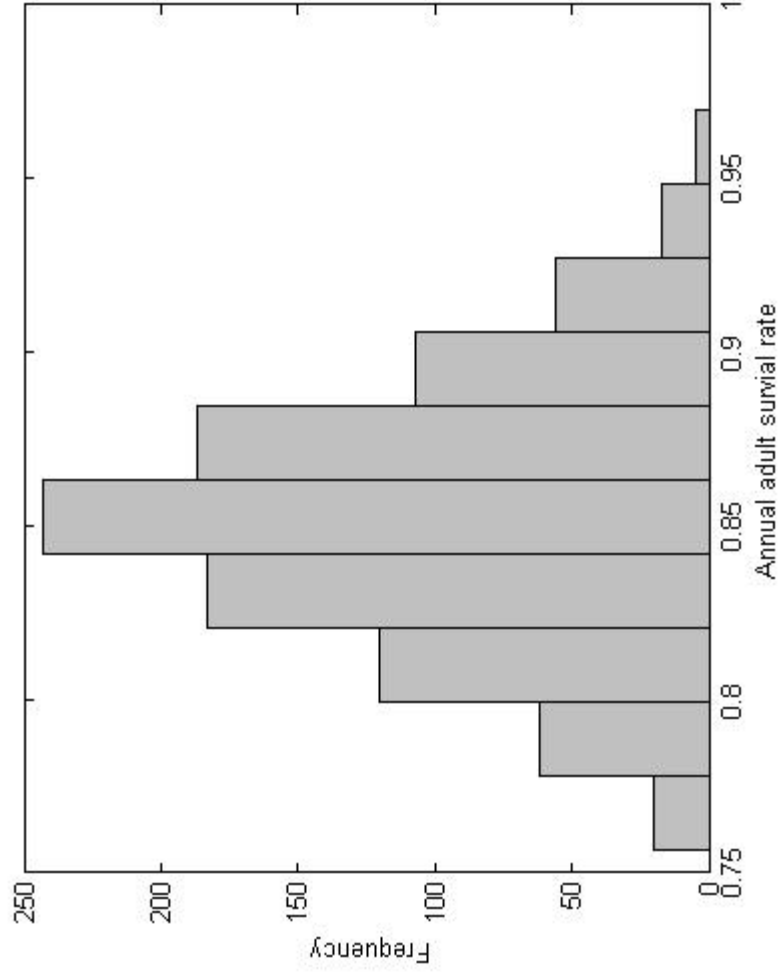


Figure 3.4. Projection of model 1 of nests laid per year for the 50 year projection. The model was initialized at 5000 nests in year 1 for all levels of nests/season.

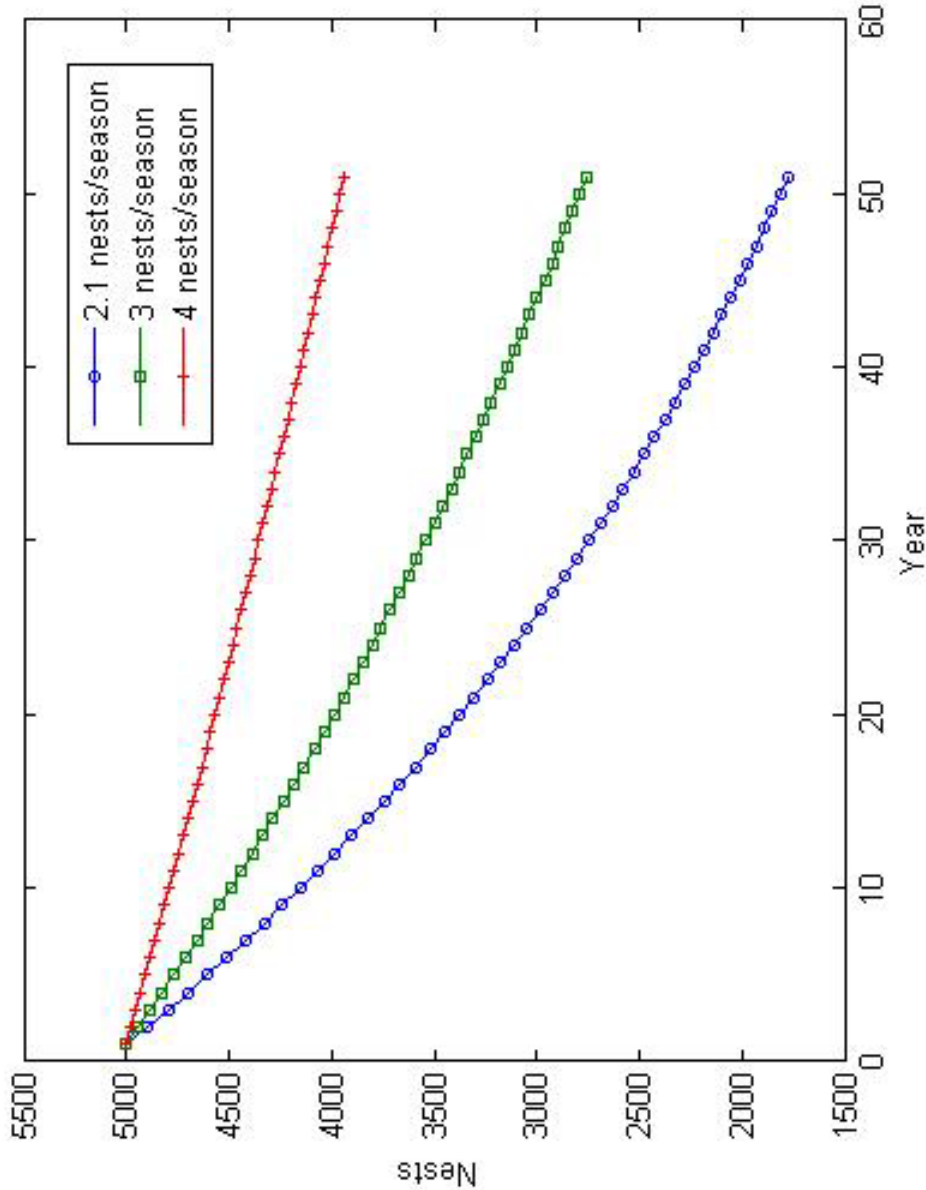


Figure 3.5. Projection of model 1 of breeders per year for the 50 years projection, initialized with 5000 nests in year 1.

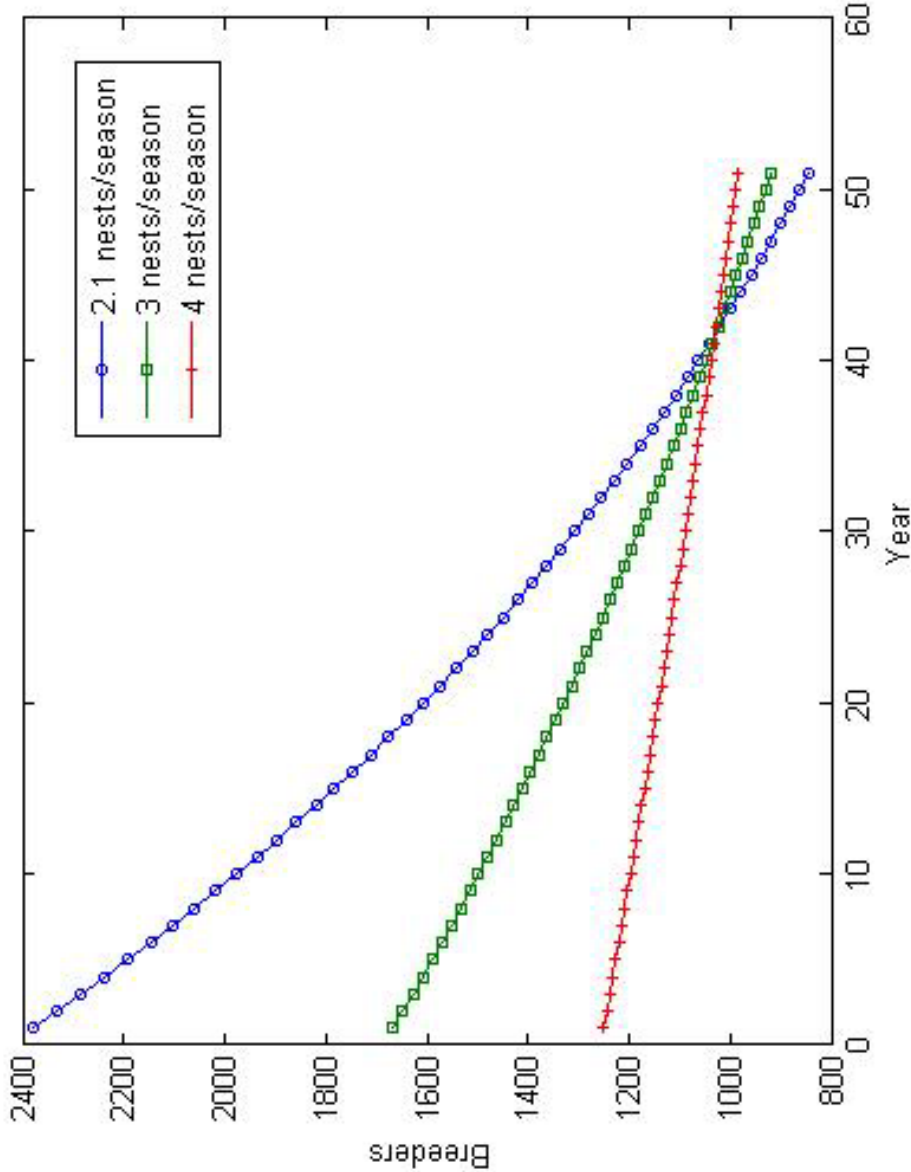


Figure 3.6. Simulation of model 2, at 2.1 nests/season, for 1000 runs. The nesting recovery threshold was defined as 12,800 nests/season.

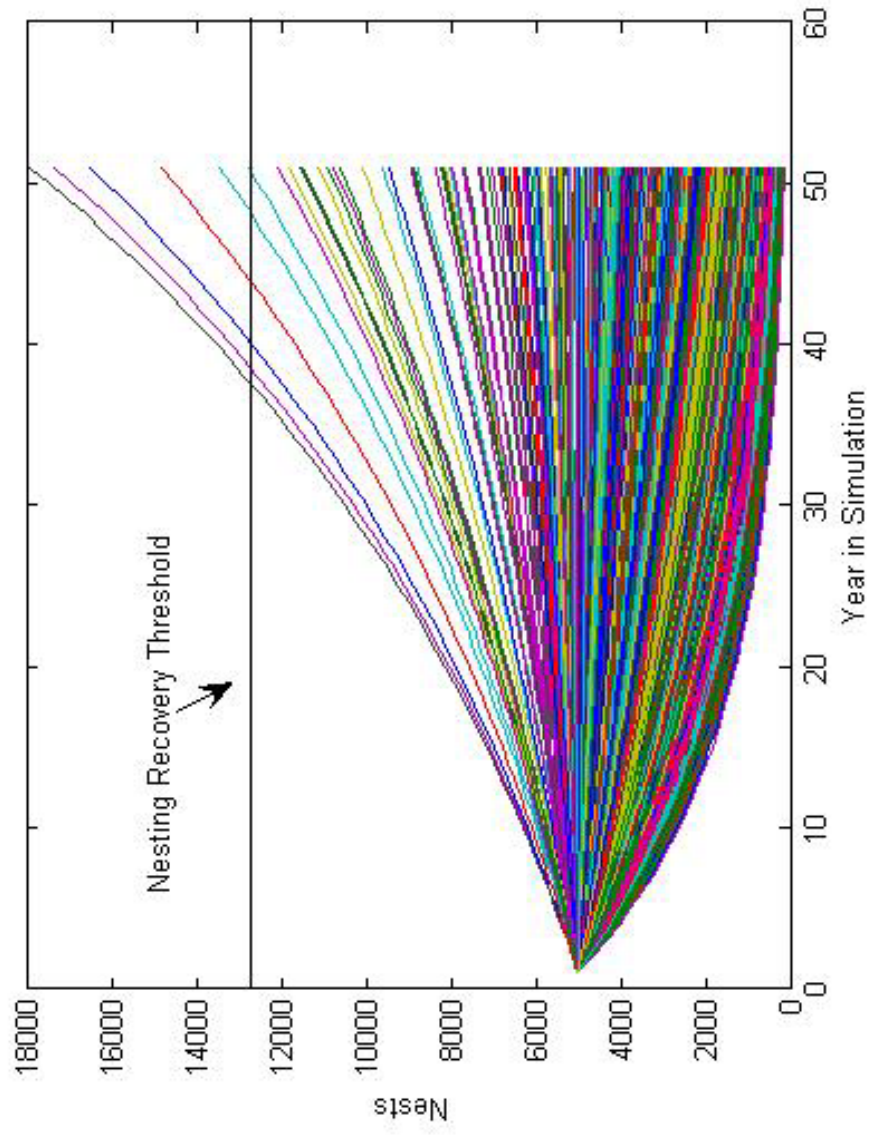


Figure 3.8. Box plot of annual population growth rate for model 3, including estimation error around adult survival. Outliers are denoted by “+”.

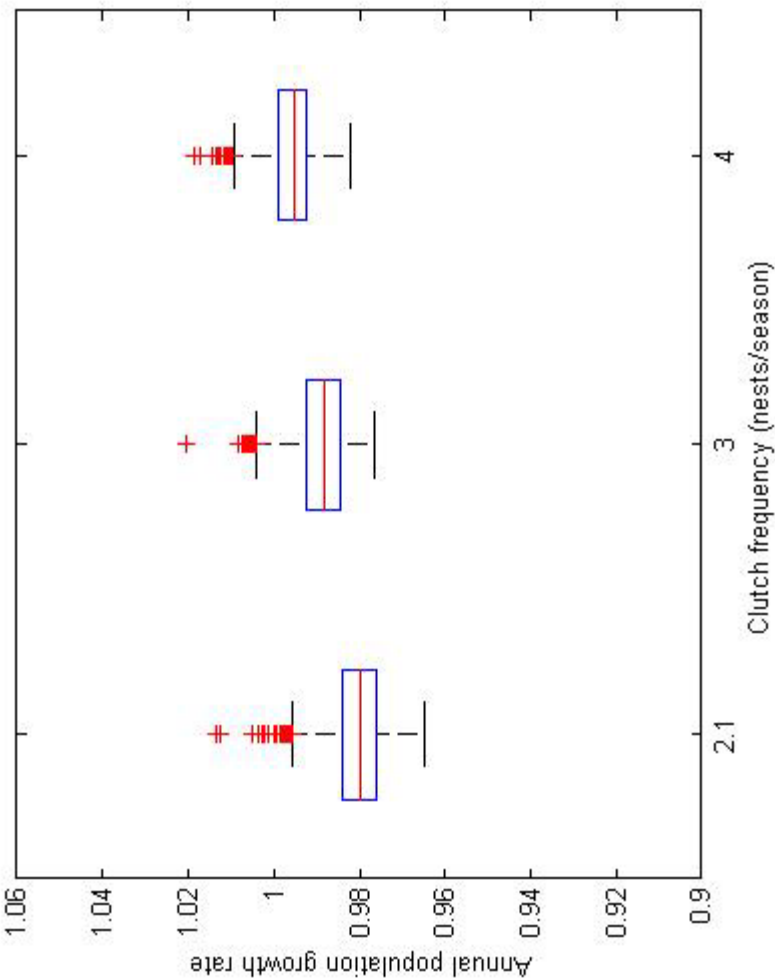


Figure 3. 9. Elasticity of lambda (annual population growth rate) to proportional changes in annual survival rates for stage classes for two loggerhead models (model 1 and model 2 at 2.1 nests/season).

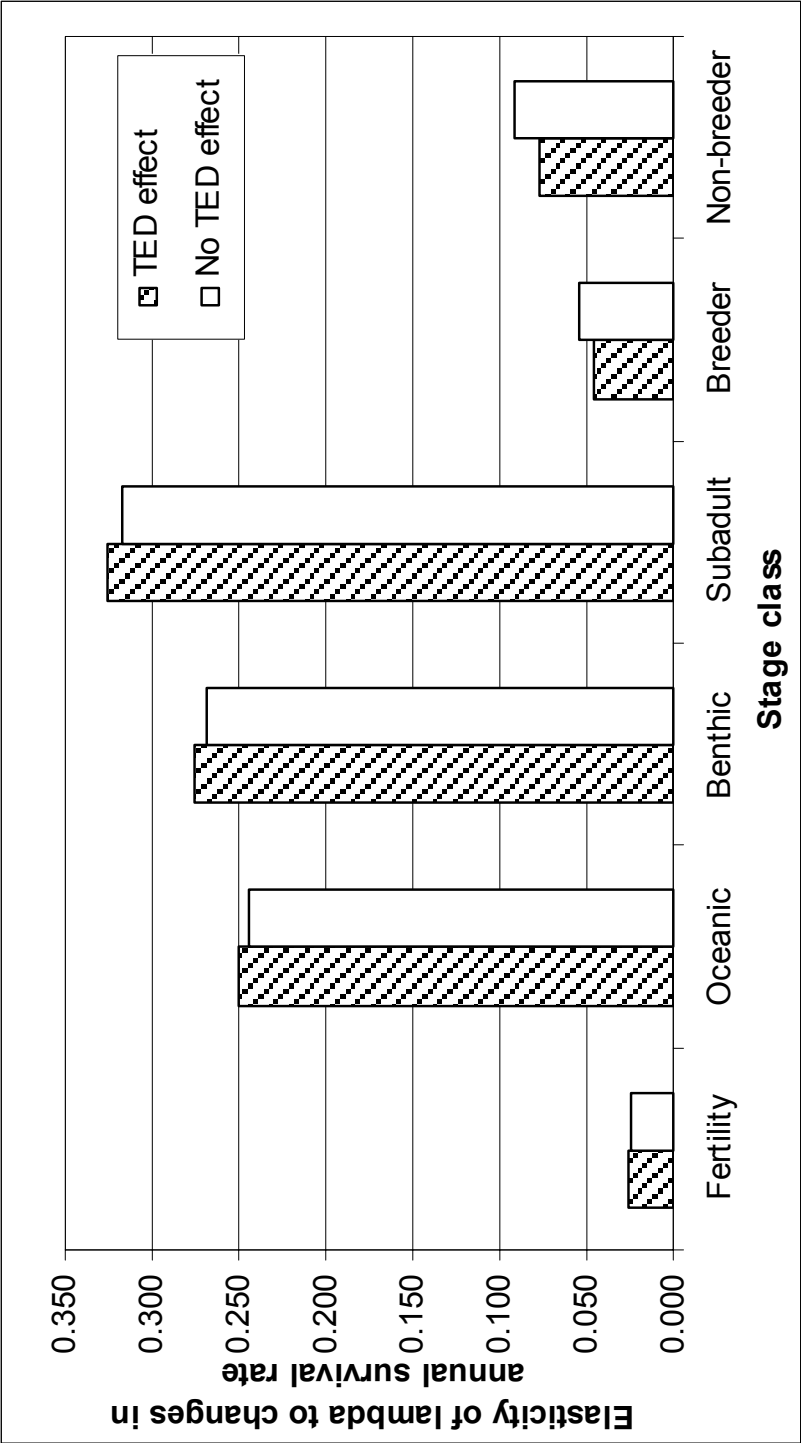


Figure 3.10. Box plot of annual population growth rate for model 4, including estimation error around benthic juvenile and adult survival. Outliers are denoted by “+”.

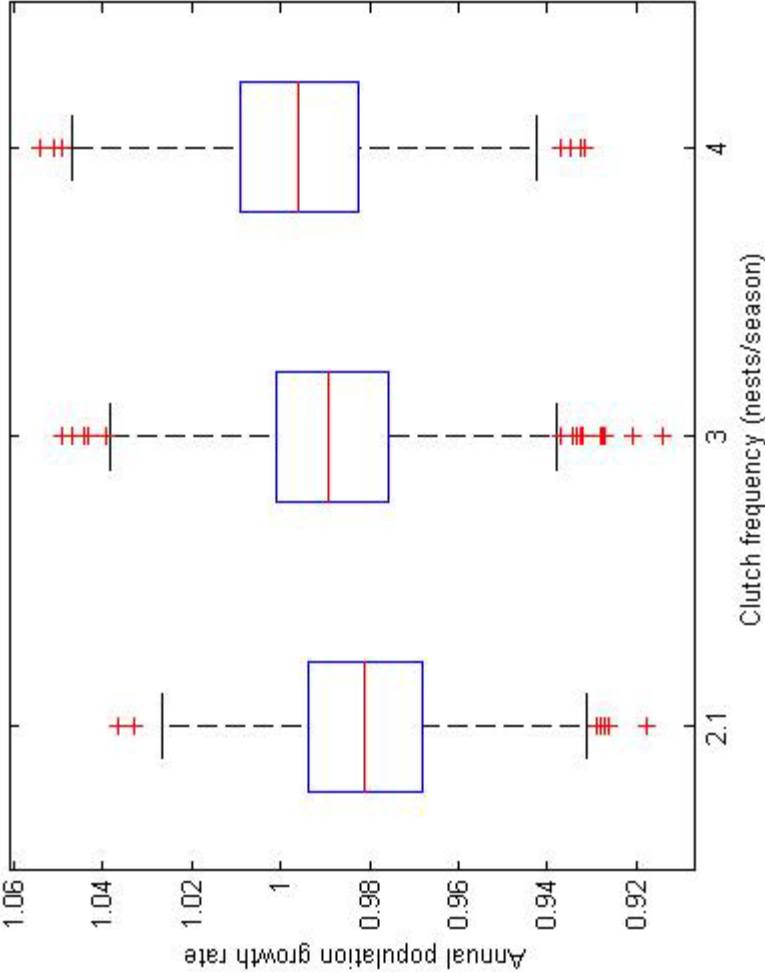


Figure 3.11. Projection of model 5 of nests laid per year for a 50 year projection, initialized at 5000 nests in year 1.

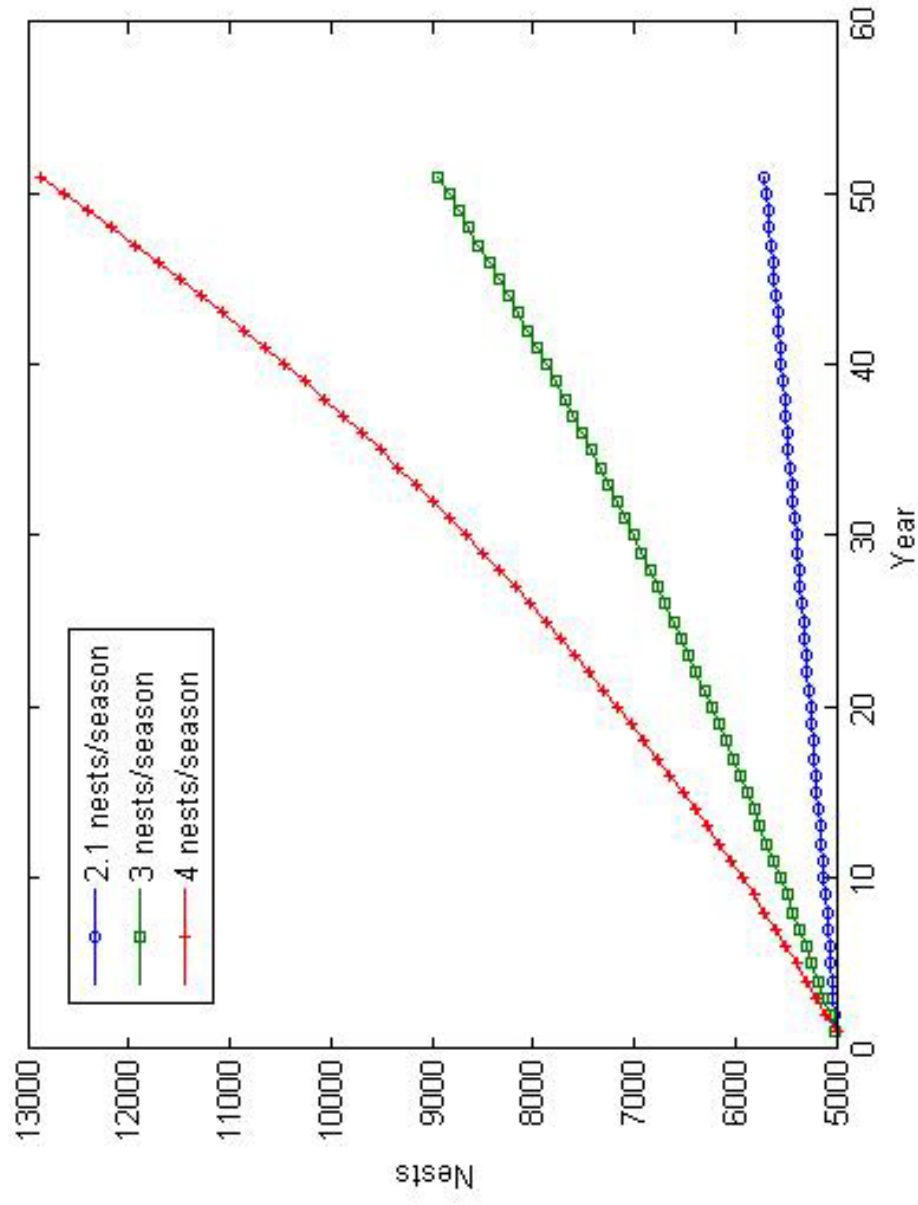


Figure 3.12. Projection of model 5 of breeders per year for a 50 year projection, initialized with 5000 nests in year 1.

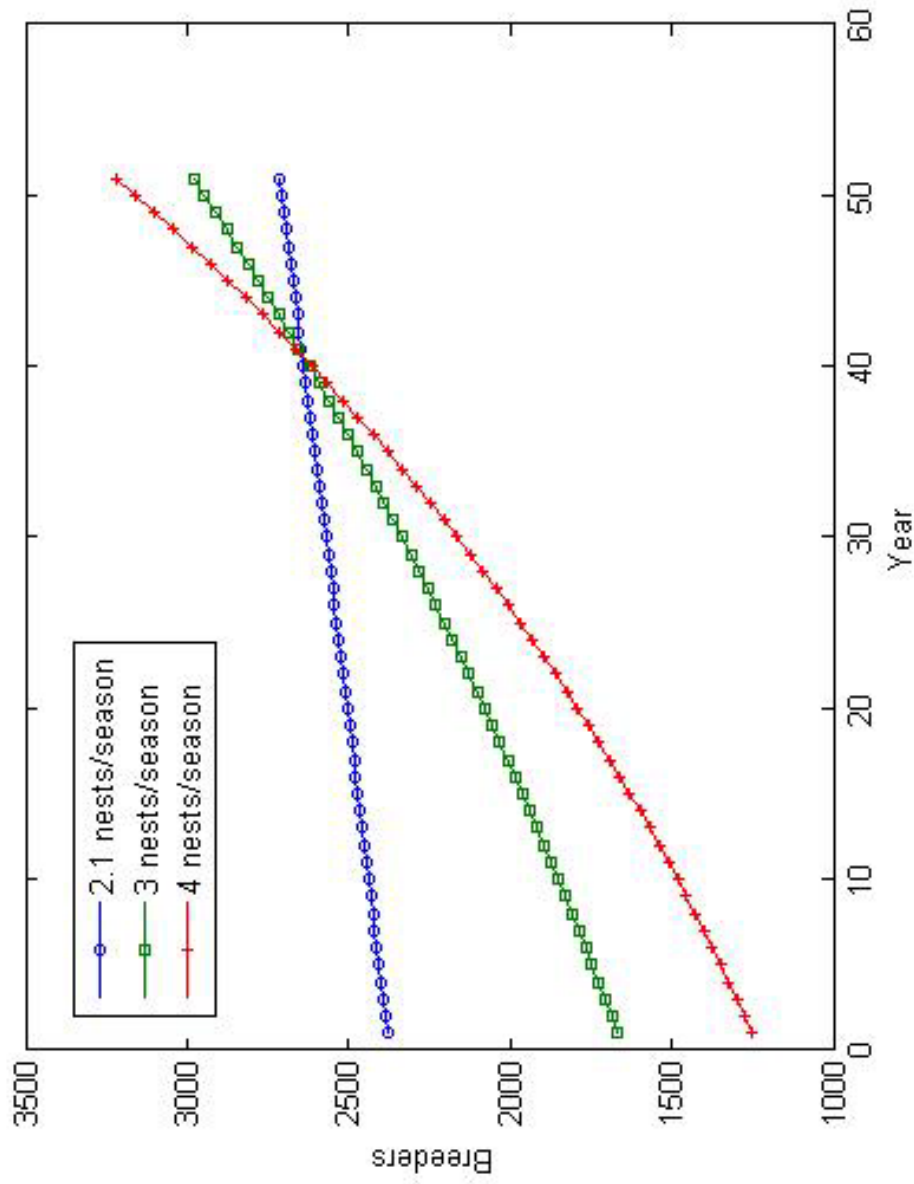


Figure 3.13. Box plot of annual population growth rate for model 6, including the TED effect and estimation error around benthic juvenile and adult survival rates. Outliers are denoted by “+”.

